THE THERMAL BIOLOGY OF THE TURKS AND CAICOS ISLANDS ROCK IGUANA *CYCLURA CARINATA*

By

DAVID LESLIE AUTH

A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL OF
THE UNIVERSITY OF FLORIDA
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1980

ACKNOWLEDGEMENTS

I am grateful to numerous members of the faculty of the University of Florida: to Walter Auffenberg, Lewis Berner, Robert DeWitt, Thomas Emmel, and Howard Wallace, for their faith in my competence as a zoologist; to Archie Carr, John Kaufmann, Brian McNab, and Hugh Popenoe, for their forebearance, patience, and time as members of the Ph.D. committee; to John Anderson, John Brookbank, William E. S. Carr, Thomas Hollinger, David Johnston, James Nation, Michael O'Rand, and Ronald Wolff, for the pleasure of being a laboratory teaching assistant for their courses; to Gerald Olsen, for introducing me to the anesthetic halothane; to Robert DeWitt, John Ewel, Brian McNab, and Horst Schwassmann, for use of equipment; and to James Heath, whose work and brief personal contact started my interest in lizard thermoregulation.

I thank the New York Zoological Society for the financial support necessary to accomplish the research. The University of Florida has provided extensive support throughout my graduate career, in the form of teaching assistantships in the Zoology Department and the College of Veterinary Medicine. Educational assistance through the G.I. Bill and the Naval Reserve proved essential.

John Iverson introduced me to the habitats and habits of *Cyclura carinata* and continued to aid me in many ways during the study. Diderot Dicca, Dagmar Werner, and Thomas Wiewandt willingly shared their knowledge of other species of *Cyclura*.

C. W. (Liam) Maguire and Bill and Ginny Cowles of the Meridian Club, Pine Cay, permitted me to stay for practically nothing in the lap of luxury while working in the field. They were most hospitable hosts. Gaston Decker, Chuck and Cathy Hesse, and Francoise de Rouvray, also of Pine Cay, helped me in many ways.

Alan Bolten, Jon Baskin, and William Link were superior companions and considerate office mates. Alexis Arends, Susan Barnard, Hugh Ellis, Michael May, Ken Prestwich, and Perran Ross gave needed technical assistance. Karen Bjorndal, David Deitz, Dale Jackson, Howard Kochman, Anne and Peter Meylan, and Michael Marshall all provided moral support.

I owe the greatest debt to my mother, Mildred G. Auth, my father, Eugene F. Auth, and my brothers, Ronald and Dennis.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS. ii

LIST OF TABLES. vii

LIST OF FIGURES ix

ABSTRACT. xiv

INTRODUCTION. 1

METHODS AND MATERIALS 7

ECOLOGICAL ASPECTS OF THE THERMAL BIOLOGY OF *CYCLURA CARINATA* . . . 24

Climate of Water Cay 24
Diel Body Temperature Cycle of a Heliothermic Lizard 31
Regulating Phase Body Temperature in the Field 34
Temporary Hyperthermia and Hypothermia 44
The Relationship of Pertinent Environmental Variables to Regulating Phase Body Temperatures 55

Season 55
Habitat Complexity 62
Cloud Cover. 67
Shaded Air Temperature 73
Substrate Temperature. 75

Patterns of Heat Transfer between Penned Iguanas and their Environment: The Three-Transmitter Study. 78
Statistical Analyses of Regulating Phase Body Temperature. . . 89

Body Temperature Maxima and Minima 89
Skewness of Body Temperature Frequency Distribution. . . 107
Standard Deviation of Mean Body Temperature. 112

Rates of Lizard Heating and Cooling in the Field 119

Morning Heating and Regulating Phase 119
Lizard Cooling in Burrows. 125

ETHOLOGICAL ASPECTS OF THE THERMAL BIOLOGY OF *CYCLURA CARINATA*. . . 132

Lizard Activity. 132

Burrow Movement. 132
Control of Lizard Emergence and Submergence. 132

Morning Heating Phase. 146
Regulating Phase 149
Foray Movement and Body Temperature. 154
Feeding, Transmitter Passage Time, and Defecation. . . . 166
Drinking 168
Nasal Salt Gland Secretion 170
Time-Motion Study of Penned Lizards. 171

Behavioral Thermoregulation. 174

Description of Thermoregulatory Movements and Postures . 174
Shuttling Behavior 184
Sun Orientation. 187
Thigmothermia. 200
Low Body Temperature Behavior. 213
High Body Temperature Behavior 216
Head-Body Temperature Differences. 224
The Integument: Metachromatism and Reflectivity. 227
The Integument: Sensory Spots. 231

PHYSIOLOGICAL ASPECTS OF THE THERMAL BIOLOGY OF *CYCLURA CARINATA*. . 236

Heating and Cooling Rates. 236
Aerobic Metabolism 248
Heart Rate 253
Recovery from Maximum Exercise 259

DISCUSSION. 270

Body Temperature Relations 270

Comparison of *Cyclura carinata*'s Mean Body Temperature with Other Diurnal Lizards. 270
Seasonal Variation in Body Temperatures of Active Lizards. 276
Stability of the Mean Preferred Body Temperature 277
Late Afternoon Maximum Body Temperature. 279
Thermal Safety Margins 281
Panting Threshold. 282
Body Temperature and Reproductive State. 284

Ethological Considerations 285

Lizard Activity. 285
Eurythermy vs. Stenothermy 288
Comparative Thermoregulatory Behavior of Heliothermic Lizards. 296
Complexity of Social Behavior in *Cyclura carinata* as a Function of Latitude 305
Nocturnal Lizard Aggregations. 306

Physiological Considerations 307

Aerobic vs. Anaerobic Metabolism 307
Neural Basis for Shuttling Behavior in Lizards 312

SUMMARY OF RESULTS AND CONCLUSIONS. 326

LITERATURE CITED. 347

BIOGRAPHICAL SKETCH 367

LIST OF TABLES

Table

1 Daily variation in relative humidity. 30

2 Summary of regulating phase body temperatures of lizards in the field. 35

3 Hyperthermia in *Cyclura carinata* in the field 47

4 A seasonal comparison of some environmental variables at Site II on Water Cay 56

5 Seasonal changes in regulating phase body temperature in the field and in the laboratory thermal gradient 57

6 Vegetational cover at Sites I and II on Water Cay 66

7 Body temperatures of *Cyclura carinata* confined to cages with two structurally different habitats. 68

8 Skewness of frequency distributions of minimum and maximum body temperatures 91

9 Means and standard deviations of minimum and maximum body temperatures of individual lizards and correlation of maximum vs. minimum and minimum vs. maximum T_b pairs . . 92

10 Linear regression analysis of daily minimum vs. maximum T_b's and mean of daily T_b minima vs. mean of daily T_b maxima for individual lizards. 101

11 Skewness and kurtosis of T_b frequency distributions 118

12 Rates of lizard heating and cooling in the field during the morning heating and regulating phases 120

13 Lizard cooling in burrows in the field. 124

14 Lizard body temperature at emergence in the field 131

15 Emergence and submergence times, temperatures, and light intensities for free-ranging lizards in the field 146

16 Possible acclimatization of lizard activity 165

17 Effect of body temperature on the feeding rate and meal size of penned *Cyclura carinata* 167

18 Time-motion study of *Cyclura carinata* in the Gainesville pen 172

19 Skin patch heating. 198

20 Estimated thermal conductance during heating and cooling of lizards in still air 240

21 Correlations of lizard behaviors with body temperature during heating and cooling in the cage and on the jig . . . 245

22 Recovery oxygen for *Cyclura carinata* after seven minutes of maximum exercise 265

23 Comparison of actual mean recovery time after maximum exercise with recovery times at three hypothetical rates of oxygen utilization 267

24 Field body temperatures of diurnally active lizards 271

LIST OF FIGURES

Figure

1 Black body temperatures in the field. 25

2 Air temperature in the shade at Gainesville, Florida and Grand Turk, British West Indies 26

3 Mean maximum wind speed at Site II in July. 28

4 Monthly precipitation on Grand Turk, British West Indies. . 29

5 Body temperature record of Lizard 2 on February 10, 1976. . 32

6 Summary of field body temperatures during the regulating phase 45

7 Lizard hyperthermia and hypothermia during the regulating phase 46

8 Patterns of regulating phase body temperature and distance traveled in *Cyclura carinata* in a laboratory thermal gradient. 51

9 Hypothermia in a free-ranging lizard. 54

10 Seasonal change in *Cyclura* regulating phase body temperature in the Caicos and Gainesville, Florida. 59

11 Relationship of mean body temperatures in the field and the thermal gradient for active lizards from several families. 61

12 Influence of habitat on body temperature. 65

13 Effect of cloud cover on mean regulating phase body temperature 69

14 Effect of overcast duration on lizard body temperature change. 72

15 Correlation of lizard body temperature during the regulating phase with shaded air temperature. 74

16 Thermoregulatory flexibility. 77

17 Three transmitter record of a large male *Cyclura carinata* in the Gainesville pen on August 21, 1975. 80

18 Partitioning of heat transfer in active penned *Cyclura carinata*. 84

19 Rate of core body temperature change during the four heat transfer conditions 86

20 Correlations of the sum of daily heat transfer conditions with lizard activity and mean body temperature. 88

21 Time distributions of four combinations of maximum and minimum body temperature. 97

22 Correlations of maximum vs. minimum T_b and the mean of T_b maxima vs. minima for individual lizards 100

23 Hourly change in minimum and maximum body temperatures. . . 104

24 Timing shift of daily minimum and maximum T_b's. 106

25 Skewness of daily T_b frequency distributions. 110

26 Comparison of the level and precision of thermoregulation of *Cyclura carinata* and *Dipsosaurus dorsalis* in continuous thermal gradients 111

27 Correlation of the standard deviation of mean daily T_b with mean daily T_b. 113

28 Effect of body weight and mean T_b on the standard deviation of mean T_b. 116

29 Hourly change in the mean and standard deviation of lizard body temperature and shaded air and sand temperatures . . . 118

30 Correlation of mean rates of heating and cooling in the field with lizard body weight 124

31 Correlations of parameters describing regulating phase body temperatures 126

32 Lizard movements in a burrow. 134

33 Seasonal change in lizard emergence and submergence times . 136

34 Correlations of times of emergence and submergence with body weight in penned Gainesville lizards 140

35 Gradual reentrainment of lizard emergence time after release 145

36 Lizard activity during the morning heating phase. 148

37 Daily and seasonal variation in activity. 151

38 Variable inhibitory effectiveness of cloud cover on lizard activity 155

39 Influence of cloud cover on the length of lizard forays and the mean rate of travel during forays 159

40 Correlations of foray length and rate of travel with mean body temperature. 161

41 Body temperatures during forays 163

42 Defecation body temperatures and timing 169

43 Correlation of lizard mobility with confinement area. . . . 173

44 Thermoregulatory motions and postures of *Cyclura carinata* . 175

45 Lizard shuttling in the summer field cages. 185

46 Midday depression of shade seeking body temperature 188

47 Lizard orientation to a heat lamp during heating and cooling in the photothigmotron. 189

48 Positive and negative orientation during lizard heating and cooling 192

49 Daily and seasonal variation in sun orientation in the Gainesville pen 195

50 Left vs. right side sun orientation in the Gainesville pen 196

51 Daily change in the pattern of travel during forays 199

52 Participation of the lizard's head, neck, and legs in the reduction of substrate contact. 203

53 Relative importance of lateral compression of the trunk vs. head, neck, and trunk elevation 205

54 Conductive and convective heating and cooling of a single *Cyclura carinata*. 206

55 Conductive heating and cooling of a single *Cyclura carinata*, with and without simultaneous radiative heating with a heat lamp. 209

56 Thigmothermic responses of a single *Cyclura carinata* to periods of increasing, stable, and decreasing substrate temperature 212

57 Behavioral responses of *Cyclura carinata* at low body temperatures. 214

58 Daily adjustment of the panting setpoint to changing heat input. 220

59 Correlation of total panting time with head and gut thermal lag times 222

60 Head-body temperature differences during heating and cooling of a 1790 g male *Cyclura carinata* in the Gainesville rooftop arena 226

61 Integumental and substrate reflectivities 228

62 Density of sensory spots on different parts of the lizard body surface. 234

63 Heating and cooling rates of a 1435 g male *Cyclura carinata* in a constant temperature chamber. 239

64 Breathing rates of lizards during heating and cooling in a constant temperature chamber. 247

65 Correlation of resting and maximum oxygen consumption with body temperature 250

66 Analyses of aerobic metabolism. 252

67 Heart rate as a function of body temperature. 254

68 Heart rate analyses 256

69 Relationship of oxygen consumption to heart rate at different body temperatures 257

70 Temporal pattern of body movements while struggling to escape. 260

71 Effect of body temperature on the rate of recovery from seven minutes of maximum activity 263

72 Early and late phase recovery from maximum exercise in *Cyclura carinata* at different body temperatures 269

73 Summary of body temperatures of selected behaviors and physiological maxima of *Cyclura carinata*. 293

74 Effect of increasing body temperature on frequency distribution skew and standard deviation of the mean for minimum and maximum body temperatures 319

75 Hypothetical neural basis for changes observed during increasing mean body temperature in *Cyclura carinata*. . . . 324

Abstract of Dissertation Presented to the Graduate Council
of the University of Florida in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy

THE THERMAL BIOLOGY OF THE TURKS AND CAICOS ISLANDS ROCK IGUANA *CYCLURA CARINATA*

By

David Leslie Auth

June, 1980

Chairman: Walter Auffenberg
Major Department: Zoology

The ecological, ethological, and physiological thermal biology of *Cyclura carinata*, a large, tropical, herbivorous iguanine lizard, was investigated on Water Cay in the Caicos Islands and in Gainesville, Florida. The study lasted from June, 1974, until September, 1976, and included four field trips totaling twenty weeks.

Far-field transmitters were placed in the coelom or gut of free-ranging adult iguanas (675-1864 g) for long-term monitoring of core body temperature (T_b) in the field. Mean regulating phase T_b ranged from 38.0 to 39.7 C (February-October), quite high compared with most other iguanids. Stenothermia was pronounced, with a mean, regulating phase T_b range of only 3.3 C. Maximum voluntary T_b, 43.8 C, was only 2.4 C below the CTMax. The CTMin, 12.8 C, almost equalled the lowest recorded environmental temperature.

Iguanas were initially hyperthermic in both the field and a thermal gradient, the former the possible result of bacterial infection or a transmitter meal and the latter of thermoregulatory learning.

Individual differences in regulating phase T_b were partially due to variable vegetational cover and, perhaps, egg development in females. Mean operant T_b's did not correlate perfectly with seasonal change in the ambient thermal environment. Mean regulating phase field T_b exceeded mean preferred T_b. The latter did not change with Gainesville seasonal acclimatization, whereas winter variance of mean T_b was less than summer variance in both field and thermal gradient.

Mean regulating phase T_b was inversely correlated with cloud cover time, the correlation improving with seasonal cooling. T_b was nearly independent of shaded air temperature.

Heat transfer through the dorsal and ventral body was examined using three transmitter placements on penned iguanas. Heat was usually gained dorsally and lost ventrally; iguanas were thigmothermic only 20.7 percent of their active period, usually in combination with heliothermia.

Individual frequency distributions of regulating phase maximum and minimum T_b's were commonly skewed positively and negatively, respectively, whereas inclusive individual distributions were usually negatively skewed. Standard deviations were slightly but not significantly greater for mean minimum than mean maximum T_b's. Change in T_b between any two consecutive maxima was positively correlated with change in two consecutive minima, with the first minimum immediately before or after the first maximum. Individual mean maximum and minimum T_b's were directly and linearly correlated, the regression line extrapolating to approximately the maximum voluntary tolerance. These results are discussed in terms of dual-limit thermoregulation.

Iguanas were diurnally active all year and rarely escaped into burrows due to overheating. Mean regulating phase heating was 1.15

times faster than cooling and 3.0 times slower than heating during morning basking. Iguanas also heated faster than they cooled in a constant temperature chamber, both when restrained and when permitted to move about. Maximum T_b commonly occurred during late afternoon basking. This and other results indicate that surface rather than core body temperature is regulated.

Both length and rate of travel were independent of mean T_b between 35.0 and 40.5 C. Arboreal climbing, burrow excavation, defecation, drinking, feeding, nasal salt gland secretion, and panting were also examined in relation to mean T_b.

Thermoregulatory behaviors and postures were described. A photothigmotron was constructed to quantify iguana light shadow and substrate contact in a controlled thermal environment. Shuttling and sun orientation were examined. A time-motion study revealed the low activity rate of penned iguanas and activity partitioning between foraging, social, and thermoregulatory behaviors. Thermoregulatory behavior was quite similar to other heliothermic iguanids.

Resting and maximum oxygen consumption, and heart rate and oxygen consumption during recovery from maximum exercise were determined at different T_b's. Iguanas fatigued rapidly during maximum exercise, yet rarely developed large oxygen debts in the field. Heart rate increment, initial rate of recovery, and oxygen scope were greater in the preferred T_b range.

INTRODUCTION

Although much is known regarding the thermal biology of small lizard species (see Heatwole 1976 for a review), large lizard species, because of their rarity in numbers and usual distribution in isolated areas, have received lesser attention. This is unfortunate, for large mass confers certain advantages and disadvantages due to low heating and cooling rates. This study investigates the thermal biology of a species of rock iguana in the genus *Cyclura* Harlan, one of nine genera in the subfamily Iguaninae (Avery and Tanner 1971). Although the genus includes some of the largest lizards in the world, *Cyclura carinata* is one of the smaller members (maximum weight of 1,864 g for males, 1,135 g for females).

Preliminary observations by Auffenberg (personal communication) in 1973 indicated that *Cyclura carinata* probably had a fairly high diurnal operant or eccritic body temperature (T_b). This, coupled with large size and a herbivorous diet, uncommon in lizards, suggested that its thermal biology could in some ways be unique. A great deal of thermally related data had already been collected for the desert iguana, *Dipsosaurus dorsalis*, a small herbivorous lizard of the North American Southwest with a very high preferred T_b (Porter *et al.* 1973). Thermally related comparisons of *Cyclura carinata* with this species as well as with the larger iguanines, *Amblyrhynchus cristatus* (White 1973), *Iguana iguana* (McGinnis and Brown 1966), and *Sauromalus obesus* (Johnson 1965) seemed worthwhile.

Continuous monitoring of the T_b of free-ranging lizards in the field using radio-telemetry forms the basis for the present study. This

approach has only rarely been followed for large lizards (Stebbins and Barwick 1968, McNab and Auffenberg 1976).

The natural history of *Cyclura carinata* was examined simultaneously from four directions by Dr. Auffenberg (feeding strategy), John Iverson (autecology and ethology) and myself, under a grant from the New York Zoological Society. The field site was located primarily on Pine and Water Cays, on the northwest side of the Caicos Island Bank. Since the goal of this research was to gain as much information as possible which could be useful in guaranteeing the species' future survival, I chose to attack the problem of thermal biology broadly, rather than emphasizing any one aspect such as thermoregulation. Ecological, ethological, and physiological approaches were taken, working only at the organismic level and using free-ranging field, controlled field, and laboratory studies. This synthetic approach has been utilized rather successfully by Grenot (1976) for *Uromatix acanthinurus*, another fairly large herbivorous lizard.

The field ecological approach to *Cyclura carinata*'s thermal biology depends on a thorough understanding of the thermal environment in which the lizard lives. This means that cloud cover, wind speed, black body temperature, shaded air temperature, and substrate temperature have to be monitored daily and seasonally as well as the lizard's body temperature and its thermally related behavior. Then, environmentally related questions can be answered. How does the lizard respond to the rather constant easterly winds? Are these xeric habitat animals able to stay out of their burrows even during the hottest part of the summer day or are they forced underground, as is the smaller

Dipsosaurus dorsalis (Porter *et al.* 1973)? Is T_b independent of shaded air temperature, as expected in a heliotherm? The populational distribution on the islands should be examined in terms of habitat types available and any variation in mean T_b with vegetational density determined. The iguana distribution (before the beginning of the study) was minimally affected by introduced mammalian competitors, since the human population was small and the only other mammal was the introduced Norway rat.

Continuous T_b records of free-ranging lizards provide a large amount of analyzable data, as shown by Stebbins and Barwick (1968) from their monitoring of a single lace monitor lizard. Maximum and minimum T_b's during the regulating phase, times of emergence and submergence, and heating and cooling rates can easily be extracted from the record. Then, many interesting questions can be addressed. How do the maxima and minima vary during the day on clear days? Does body temperature variability decrease as body weight increases? Does this variability decrease as mean T_b increases? How is mean T_b related, if at all, to reproductive state, sex, and size?

Heath (1964) and DeWitt (1967) were two of the first investigators to report a significant temperature differential between the head and body of lizards during heating and cooling, calling into question the significance of measuring just cloacal temperature and bringing up the question of what body temperature is regulated. Since then, many workers have simultaneously measured more than one body temperature in lizards (Johnson 1972, Webb, Johnson, and Firth 1972, Crawford 1972, Spray and Belkin 1972, 1973, Crawford and Barber 1974, Parmenter and

Heatwole 1975, Pough and McFarland 1976, McNab and Auffenberg 1976, Crawford *et al.* 1977). For a large lizard like *Cyclura carinata*, multiple body temperature measurements are advisable as part of the study. Head-gut and dorsal black body-gut-ventral body surface temperatures were measured to determine internal temperature differences and dorsal and ventral heat transfers with the environment, respectively. Lizards had to be confined in outdoor pens to maintain continuous visual contact, a serious problem with free-ranging lizards.

Two aspects of the ethological thermal biology of *Cyclura carinata* are investigated. The first addresses the question of how daily variation in the thermal environment and T_b influence lizard activity. Lizard movement in burrows, emergence and submergence timing, movement during the morning basking and regulating phases, feeding rate, total food consumed, passage time of transmitters through the gut, defecation timing, and secretion timing of the nasal salt gland are considered. Lizards vary considerably in the amount of time spent in actual motion. "Widely foraging" predators, such as varanids and teiids, are generally more active than "sit and wait" insect feeding iguanids (Pianka 1973). Herbivorous lizards should fall somewhere in between, if they feed on a variety of plants, since they must go to where the plants are located and then actively pick items up. The partitioning of the lizard's active time between feeding, social, and thermoregulatory movements should vary consistently between each of these three dietetic categories. Ideally, a continuous time-motion study should be conducted in the field, as accomplished for *Egernia cunninghami* by Wilson and Lee (1974). However, this proved impossible

from a fixed blind, due to vegetational density and the considerable distance traveled by adult iguanas. Penned lizards were observed instead.

The second ethological approach is to discover how *Cyclura carinata* regulates its body temperature and then to compare this behavior with that of other lizards, reported on extensively in the literature. This has traditionally been the emphasis of lizard thermal biology studies, since the time of Cowles and Bogert (1944). The roles of thermoregulatory postures were comprehensively catalogued in a qualitative manner, similar to Brattstrom's work on *Amphibolurus barbatus* (1971) and Greenberg's on *Sceloporus cyanogenys* (1977).. Some of the behaviors were quantified under controlled field and laboratory conditions. A laboratory device was built to quantify the degree of sun orientation and thigmothermia, using a photographic technique similar to Heath's for *Phynosoma* (1965). I did not attempt to find out to what extent body posture controlled T_b under a defined set of thermal conditions, as Muth (1977b) and Porter and James (1979) have recently done.

Lizards usually heat faster than they cool (Bartholomew and Tucker 1963, 1964, Morgareidge and White 1969, Weathers 1970, Weathers and Morgareidge 1971, Weathers 1971, Baker *et al.* 1972, Ellis and Ross 1977). This is attributed to increased peripheral blood flow during heating. The ratio of heating to cooling rate increases as body mass increases in the American alligator, to the extent that while hatchlings heat and cool at about the same rate, a 1000 kg adult would theoretically heat nearly three times faster than it cools (Smith 1979). The testing

of *Cyclura carinata* is justified on comparative grounds and because of its large size, especially since the data obtained complement the heating and cooling rate results for the species in the field.

Many rate processes become somewhat temperature independent in reptilian preferred T_b ranges (see Dawson 1975 for a review). Selected physiological parameters--resting and maximum oxygen consumption, resting and maximum heart rate, and oxygen consumption during recovery from maximum exercise--were measured in *Cyclura carinata* to see how they varied with T_b. The study of recovery from maximum exercise was especially interesting, since the amounts and kinds of voluntarily tolerated, strenuous activity the species engaged in were observed in the field. Bennett's methodology (1972) for his comparison of oxygen consumption, oxygen debt, and heart rate in *Varanus gouldii* and *Sauromalus hispidus* was closely followed, permitting comparison with results obtained for *Cyclura*.

METHODS AND MATERIALS

The field study site was located in the Caicos Islands, between 21° and 22° North latitude and 71° 30' and 72° 30' West longitude, approximately 150 km north of Hispaniola and 890 km southeast of Miami, Florida. Pine Cay was the base of operations, a privately owned island with excellent lodging, potable water, an air strip, and a large population of *Cyclura carinata* (as of August 1973). Field work was conducted primarily on Water Cay, connected by a traversable sand bridge to Pine Cay. Iguana density was adequate here at the beginning of the study, no human habitation was present, and bulldozed paths provided easy access to most areas at the northeast end of the island. The two islands are located on the northern perimeter of the triangularly shaped Caicos Bank, a shoal with a northern base of 125 km and a southerly directed altitude of 75 km. Water Cay has an area of approximately 225 ha, with a leeward northwestern sandy beach, a windward eastern rocky limestone coast, and a southern mangrove swamp. The height and density of the vegetation increases with island age and soil depth and quality from the northwestern to the southeastern side of the island. The highest point is approximately five meters above sea level.

I spent a total of 140 days in the field during four trips: June 1-July 28, 1974; September 30-November 4, 1975; February 4-23, 1976; and August 17-September 11, 1976.

Two field sites were chosen on the eastern end of Water Cay. Site I was in level, sandy, Semiopen Scrub, 600 m from the NE side and 275 m from

the NW side of the island. Site II was in Dense Scrub, with Rocky Coppice bordering the Pine-Water Cay inlet, 200 m from the SE corner of the island (see Auffenberg, in prep., for descriptions of vegetation types). Work was confined to approximately one hectare at each site. Site I bordered a bulldozed road and Site II was crisscrossed by an interconnected road network.

A moderately large hotel complex was completed on Pine Cay in the summer of 1973. By the time of my first trip, iguana populations had already declined on both Pine and Water Cays due to predation by man, dogs, and feral cats. The subsequent collapse of the population on Pine Cay has been documented by Iverson (1977). *Cyclura* density at Site II was estimated at 10 adults per ha in July, 1974. Density was somewhat less at Site I. Iguanas had practically disappeared from Site I by September, 1975, necessitating a concentration of effort at Site II. Iguanas had been extirpated from Site II by August, 1976, resulting in a shift of field work further southwest along Water Cay and to Fort George Cay, just north of Pine Cay. Due to the small number of hatchling and juvenile iguanas, the study had to be restricted to adults.

Eleven male ($\bar{X}$ = 993 g, 435-1715) and four female ($\bar{X}$ = 748 g, 528-1135) iguanas were brought to Gainesville, where they were kept in two outdoor galvanized sheet metal pens. One pen was circular, enclosing an area of 16 m^2, and the other was rectangular, enclosing 18 m^2. Eight plywood boxes, each measuring 40 cm wide by 40 cm long by 10 cm high, were perched on concrete blocks and provided shade, shelter, and basking platforms. Substrates were beach sand and grass in the circular and rectangular pens, respectively. From October 1 to March 30, the

pens were partially or completely covered with 4 ml polyurethane plastic to increase temperatures. An electric forced air heater kept temperatures above freezing on exceptionally cold nights. The captives were fed bananas, green beans, white grapes, and fish-flavored catfood.

Several environmental variables were monitored in the field. Measurements were taken hourly at a single location near the blind at Sites I and II, where an open, sun exposed area bordered an area of fairly dense vegetation. Changing temperatures between readings were estimated to occur linearly. Substrate temperatures were taken on dry sand with a Number 421 banjo probe attached to a Model 46 Tele-Thermometer (Yellow Springs Instrument Co.). Air temperatures were taken at a height of 2-3 cm with a Number 405 air probe. A black body for estimating daily variations in solar heat input was constructed by placing a mercury thermometer in a groove carved in a balsa wood block. The block was then covered with a thin brass plate (0.4 mm) and coated with flat black paint. A record was kept of the times the sun was obscured by clouds. Light intensity was measured with a Type 213 light meter (General Electric) directed from a height of 20 cm at a piece of white painted cardboard placed on the ground. Instantaneous wind speed was measured with a Dwyer wind meter. Average wind speed was determined over a one minute period with an Air Meter Model W131 (Weather Measure Corp.). Relative humidity was measured with a sling psychrometer.

Core body temperatures of free-ranging iguanas were measured with Model L far-field transmitters (Mini-Mitter Co.). The transmitter was a crystal-controlled blocking oscillator operating in the citizen's band range (27 MHz). Osgood and Weigl (1972) describe the circuit diagram

and construction. The signal, a series of beeps increasing in frequency with temperature, was received with a Model HA-420 three-channel walkie-talkie (Lafayette) with an attached beat frequency oscillator. Transmitter range was approximately 200-300 feet, depending on the topography. Accuracy was $\pm$ 0.5 C. The transmitter was powered by two hearing aid batteries (Mallory MS 76), which had a working life of one to two months. The transmitter was embedded in epoxy resin and enclosed in a plastic capsule. The capsule was then coated with a mixture of 50 percent paraffin and 50 percent beeswax, followed by dental acrylic (NuWeld, I.D. Caulk Co.). The package weighed about 15 g and was smaller (1.7 by 3.7 cm) than a *Cyclura* egg. A single mercury thermometer (Scientific Products), checked for accuracy against a NBS certified bomb calorimeter thermometer (Parr Instrument Co.), was used to calibrate all transmitters used in this study. Most transmitters were recovered after the monitoring period. Drift never exceeded 0.5 C.

During the summer field trip of 1974, a transmitter was implanted in each of eight adult iguanas. The operation was performed during the night of the day of capture. The lizard was fastened to a wooden jig similar to that used by Bartholomew and Tucker (1963). The individual was then placed in a large freezer cabinet until body temperature had fallen to 2-5 C. T_b was monitored intestinally with a Tele-Thermometer Probe Number 701 inserted approximately 10 cm into the distal colon and taped to the tail. The individual was kept on ice during the operation. The transmitter was inserted through a dorsoventral incision made on the right lateral abdominal wall about 1 cm anterior to the rear leg. The incision was closed with nylon fishing line.

Individuals were released the day following the operation and monitored immediately. During subsequent field trips, transmitters were placed in the gut immediately after capture. A gauze pad soaked with halothane (Ayerst Laboratories) was positioned at the bottom of a 250 ml beaker. See McDonald (1976) for a discussion of this inhalation anesthetic. The beaker was then slipped over the lizard's head. A rubber apron taped to the mouth of the beaker extended over the forelegs, reducing the rate of loss of gas anesthetic. Lizards were usually apneustic when the mask was initially placed over their heads, the duration of apnea being inversely correlated with body temperature. The drug took effect within a minute after breathing commenced. Complete anesthesia lasted between five and ten minutes, and recovery was seemingly complete within an hour. All individuals were weighed (Ohaus Dial Spring Scale), measured (snout-vent and total length), examined for scars and ectoparasites, and marked on both sides of the trunk with a bright orange Arabic numeral (Aero-gloss paint, Pactra Industries).

The body temperatures of eleven different, free-ranging adult iguanas were monitored during the study (10 males, 1 female). Two males were monitored on two separate trips. Recording periods extended from three to twenty days. Temperature readings were taken every five to fifteen minutes from before the individual emerged up to two hours after it submerged for the day.

I observed and monitored iguanas from a blind during the first field trip. Lizards were attracted to the vicinity with a sardine bait and noosed from inside the blind. Less timid individuals were noosed without bait and blind.

Iguanas were less timid during the second and third trips, permitting more thorough observation of specific individuals by continuous tracking (6 adult males tracked 1-6 days, $\bar{X}$ = 4 days). Following initial transmitter placement, iguanas were monitored without further visual contact until the start of the second or third day. Since iguanas usually retreated into their burrows when disturbed during the initial basking period, visual contact was always delayed for a time after emergence. I crawled along behind the lizard at a distance of approximately five meters during its feeding forays. Visual contact was intermittently lost when the individual moved off into dense scrub. The lizard was usually quickly resighted by following the same direction of travel. Signal strength, as perceived by the human ear, reached a maximum approximately three meters from the transmitter. Bushes along the route of travel were flagged with orange plastic tape marked with the date and time. A crude map of the route was recorded in a notebook, along with observations of the individual's behavior. The locations of the flags were later marked on a detailed map of the site. Average rates of travel and distances traveled could then be calculated at leisure.

Near-field transmitters, built according to Mackay (1970), were used during the study. They were cylindrically shaped, measuring approximately 1 by 3 cm and weighing 4 to 6 g. The signal, a series of clicks increasing in frequency with temperature, was received at a maximum distance of one meter with an AM transistor radio (50-160 KHz). The package was sealed in the same manner as the far-field transmitters.

Iguana movement in the burrow and T_b were monitored simultaneously during the second and third trips by placing both a

near-field and a far-field transmitter in the gut of a single large male. After the lizard submerged for the night, its position was located by moving the AM radio to where the signal was strongest. The radio was again placed directly over the lizard early the next morning prior to emergence. The signal was monitored at the blind six to nine meters away from the burrow by listening through an earplug connected to the radio. When the lizard moved, indicated by fading or loss of the signal, I quietly moved the radio to the lizard's new position and returned to the blind. This procedure was repeated until the lizard emerged. To see how far it would submerge, the lizard was deliberately scared into its burrow at different times of day. The location of the burrow terminus was determined by digging at the end of the monitoring period.

In June of 1974 body temperatures of four iguanas were monitored two at a time in two field cages at Site I. The cages were constructed of quarter inch hardware cloth in the shape of a cylinder 1 m high by 2 m long. Two, 15 cm diameter, 1 m long cylinders were attached to one end of each cage and covered with sand to simulate burrows. Shellac coated copper wire was wrapped around the entire cage to act as an antenna for the near-field transmitters. Strands were approximately 10 cm apart. Each two leads were attached to a circuit breaker connected to two similar leads from wire wrapped around the ferrite antenna of the AM radio. Thus, monitoring the T_b of one lizard could be immediately followed by monitoring the second by switching circuits. Individuals were kept in a complex habitat during the first four to seven days. One-half of the cage was covered with thatch palm fronds and branches were arranged beneath the fronds inside the cage, allowing the iguana

to get nearly one meter off the ground while still remaining in the shade. The burrows provided the only shade during the next two to three days of monitoring, in what was called the simple habitat. The body temperatures of two caged and two free-ranging iguanas could be monitored simultaneously from the blind.

Preferred T_b's were determined in two thermal gradients constructed of plywood, each 2.2 m long, 0.4 m wide, and 0.6 m high, with tops covered with quarter inch hardware cloth. Two 250 w heat lamps were suspended at one end of each gradient; their height was adjusted so that the black body temperature immediately beneath them was 60 C, slightly below the lowest monthly maximum recorded in the field (63 C in February). The gradients were placed in a controlled environmental room (Environ-Room, Lab-Line Instruments, Inc.) set at an air temperature of 25 C ($\pm$ 1.0 C accuracy, air velocity next to the lizard less than 0.25 m/second). The air temperature in the cool end of the gradients gradually increased to a maximum of 28-30 C after four hours of the eight hour photoperiod. The photoperiod was centered at 1200 EST. A 40 w fluorescent bulb provided less than ten footcandles of illumination. Preferred T_b's were determined for eight adult iguanas, a group of four acclimatized to Gainesville temperatures both in July-August and December-January. Summer and winter lizards were monitored individually, for four to eight consecutive days, respectively. Monitoring commenced the day following transmitter placement. Lizards received neither food nor water while in the gradient.

Low body temperature behavior was examined in six adult *Cyclura* acclimatized to Gainesville temperatures in May. Starting at 1200-1600 (all times reported in this study are EST), the individual was cooled in

the environmental room set at an air temperature of 5-8 C. Body temperature was monitored colonically with the Tele-Thermometer. The losses of seven behavioral responses were noted as T_b decreased: 1. crawling, 2. turning over when placed on the back (critical thermal minimum), 3. maintaining a horizontal head orientation when the body was rotated about its long axis, 4. maintaining a constant field of view by rotating the head or eyes when the body was rotated laterally, 5. moving the legs when pinched while resting on the back, 6. bloating, and 7. closing and opening the eyes. Each lizard was cooled an additional 3 C, then exposed to room temperature outside the environmental room. The lizard's body temperature was again recorded as each of the seven behavioral responses was regained.

To examine the timing and degree of heat transfer through the dorsal and ventral surfaces of the iguana's body, three-transmitter experiments were run in a circular Gainesville pen in late August and early September. Two far-field transmitters were fastened with electrician's tape to the outside of a piece of television antenna cable. When the cable was wrapped around the lizard's waist just anterior to the rear legs, the transmitters were situated ventro-laterally on either side of the trunk. The cable ends were held together dorsally with a rivet. The temperature-sensitive thermistor bead, embedded in epoxy resin, was located at the end of a short probe wire extending from one end of the transmitter. One probe tip was taped to the middle of the ventral side of the cable, to monitor the body-substrate interface temperature immediately under the lizard. The other, painted flat black to monitor dorsal heat input, was suspended free in the air about 1 cm anterior to the cable and 5 mm above the middle of the lizard's lower back.

A near-field transmitter was placed in the lizard's gut. Three large males (1195, 1240, and 1260 g), monitored one at a time for a total of nine days, moved freely about the pen. Seven other iguanas were also present. Readings from the three transmitters were taken every five to ten minutes. To obtain gut temperature readings, the AM radio was taped to the end of a wooden pole and extended from outside the pen to within a meter of the lizard. Shaded air, sun-exposed sand, and black body temperatures were also measured. The lizard's behavior was observed and notes taken for later correlation with the transmitter records.

To determine whether feeding rate or meal size was significantly less immediately after morning emergence than during the higher T_b's of the regulating phase, iguanas in the Gainesville pen were presented with known weights of white grapes. Food was either placed on trays on the ground, before individuals emerged for the day, or on trays affixed to the tops of posts, after individuals had reached regulating phase body temperatures. The elevated trays were large enough for only one individual to sit on, preventing feeding by several animals on a single known weight of grapes. Also, by placing grapes on three post tops simultaneously, one feeding lizard was rarely displaced by another. Animals were fed on clear days after at least two days with no food.

Sun orientation directions of lizards were measured with a hand held Silva compass. Records were obtained in the field, the Gainesville pen, and a 2 m circular arena placed on top of the zoology building. To determine the importance of vision in sun orientation control, lizards were blindfolded by placing elliptically shaped plastic disks over their eyes and securing the disks with several layers of electrician's tape

wrapped around the head. A stretch sock, with an opening for the nostrils, was then placed over the head and taped at the neck to prevent the lizard from scratching off the tape.

A photothigmotron was built to quantify thermoregulatory postural changes in *Cyclura*. A square plywood substrate box, measuring 65 by 65 by 5 cm, was lined with Plexiglas and sealed internally with fiberglass cloth and resin. A 0.3 mm thick aluminum sheet formed the top of the inner Plexiglas box and was affixed to it with Al-40 adhesive (Devcon). A grid of 1 cm squares was scored on the exposed surface of the aluminum. The substrate box rested on a 15 gallon water bath (Precision Scientific Co.). The water bath pump was connected via Tygon tubing (Norton Plastics and Synthetics Division) to two ports drilled in the side of the substrate box. Water at the desired temperature was pumped through the entry port in the substrate box and circulated evenly via six inner exit ports pointed in different directions. A small hole was made at one corner of the aluminum top to permit pressure equalization when the pump was initially turned on. A short tube was attached externally to the rim of the hole to prevent water overflow. To confine the lizard to the aluminum substrate, a one meter high hardware cloth cage, reinforced with wooden frames at top and bottom, was placed on the substrate box. The cage top was covered with a Plexiglas sheet, on which was placed a 35 mm camera directed downward toward the aluminum grid. A single 250 w heat lamp, attached to a tripod resting on the floor, was directed slightly downward toward the side of the cage. The observer's side of the cage was covered with vinyl plastic provided with a small observation port. The photothigmotron was placed inside the Environ-room.

Before each iguana was introduced into the photothigmotron, several body areas were determined. The lizard was anesthetized with halothane and placed on a Plexiglas sheet. Outlines of the outer edge of the body and the inner area of substrate contact were marked on the sheet and later transferred to a piece of paper. Three separate measurements of each area were made planimetrically and the mean taken. Contact area of the anesthetized lizard was assumed to equal maximum contact of the free-ranging lizard. The day before the first experiment, the lizard was placed on an insulative piece of plywood resting on top of the aluminum substrate of the photothigmotron. One experiment was performed each day, starting at midday. The photoperiod was ten hours. Animals were kept in the cage for three to five experiments, during which they received neither food nor water. An hour before heating or cooling of the lizard began, the water bath pump was turned on to bring substrate temperature to the desired level. The plywood was then gently removed, shifting the individual onto the metal substrate. The heat lamp was also turned on in some experiments. Photographs of the dorsal aspect of the lizard were taken at intervals. Core body temperature was measured with a near-field transmitter placed in the digestive tract. The extent of leg and tail contact was noted, as well as how much of the anterior trunk was elevated off the substrate. The black and white photograph negatives were projected with a slide projector onto a piece of white paper and the body outline traced. The dorsal outline area was determined planimetrically. Head, anterior trunk, leg and tail noncontact areas as well as a standard correction based on the difference between the inner and outer outlines of the anesthetized

lizard were subtracted from the dorsal outline area to get the approximate contact area. This value could then be converted to a percentage of the maximum possible contact.

Head temperature was measured at two different locations, using probed near-field transmitters. The transmitter was taped to a piece of television antenna cable fastened with a rivet around the lizard's neck. In a large male monitored in the photothigmotron, the thermistor probe was inserted into the orbital venous blood sinus through a 1 mm diameter hole drilled in the skull. The probe wire was glued to the center of a circular cork disk, which was glued to the top of the head with epoxy resin. Initial placement of the probe resulted in a temporary eye bulging (also noted during cannula placement in *Phrynosoma cornutum* by Heath 1966). In a second large male, monitored in the arena atop the zoology building, the probe tip was placed just inside a slit made in the tympanic membrane. The probe wire was glued to a plastic disk, which was glued to the outside of the tympanum. Lizards were allowed to recover from implantation for three days before testing.

Skin reflectivity was determined for two *Cyclura* adults from Water Cay, one in the light and one in the dark color phase. The light phase lizard was killed by heating it above the lethal maximum body temperature and the dark phase lizard died of starvation. Epidermal-dermal squares, measuring approximately 25 mm on a side, were removed from the lizards immediately after death and placed on water-moistened filter paper. Patches were taken from the mid-dorsal, ventral pectoral, and ventral abdominal trunk and the dorsal and ventral tail just distal to the anus. Integumental reflectivities were immediately determined, using a Bausch

and Lomb Spectronic 20 Spectrophotometer with reflectometer attachment. Monochromatic reflectance was obtained at a 90° angle to the skin surface, using a magnesium carbonate block as a standard. Readings were taken between 340 and 960 nm at 20 nm intervals. Reflectivity over the same range was also determined for a common substrate on Pine and Water Cays, fused corralline sand covered with two species of blue-green algae.

To check for possible reflectance of near-infrared light (700 to 900 nm) from the integument of live *Cyclura*, two adults were photographed during daily activity in Gainesville, using Kodak Infrared Ektachrome film (Schwalm *et al.* 1977). When the camera lens is covered with a yellow filter, reflected near infrared light appears red in the developed film.

Skin patches were heated from different angles to determine whether the rate of integumental heating decreased as the radiant heat shadow caused by scale imbrication increased. The patches were removed from various locations on a single adult iguana, tacked to separate pieces of plywood, dried, and cooled to 20 C in a controlled environmental room. A YSI Probe 421 was placed under the patch to monitor the time required to heat the dried skin to 50 C with a 250 w heat lamp. Each patch was heated 11 times, with the lamp at a constant distance of 17 cm, oriented normally to the skin and at 15, 30, 45, 60, and 75° from normal, both directly anterior and posterior to the imbricate edges of the scale rows.

The histological structure of integumental "sensory spots" (Miller and Kasahara 1967) were examined in tissue sections prepared for light microscopy. Material had been fixed in formalin and transferred

to isopropyl alcohol for preservation at the Florida State Museum. Tissue blocks were taken from the lizard's rostral, labial, parietal eye, and dorsal tail regions, dehydrated in ethyl alcohol, embedded in methacrylate plastic, and sectioned at 5 micrometers thickness vertical to the skin surface. Sections were mounted serially and stained with Mayer's hematoxylin and eosin-phloxine.

Six adult iguanas were heated and cooled in a controlled environmental room (Environette, Lab-Line Instruments, Inc.). Each individual was habituated for one day to its small hardware cloth cage, placed in one Environette set at an air temperature of 20 C. Polyurethane panels enclosed three sides of the cage, reducing the air flow over the lizard's body surface to practically zero. The cage floor was also composed of polyurethane. On the second day a YSI rectal probe, coated with petroleum jelly, was inserted into the lizard's large intestine to a depth of 7-10 cm and taped to the tail. The cage was then rapidly moved to another similarly wind-baffled box in another Environette set at an air temperature of 40 C. When within 1-2 C of ambient air temperature, the lizard was rapidly transferred back to the 20 C Environette and cooled. During the third and final day in the chamber, the individual was secured in a supine posture to a wooden jig. The lizard's legs were free to move. A rectal probe was again inserted into the intestine and a banjo probe glued middorsally to measure body surface temperature. The individual was then heated and cooled again. Animals were observed continuously during heating and cooling through an observation port in the chamber door. Breathing rates were recorded intermittently. The photoperiod was ten hours. Heating began at 1300 and cooling was always over by

2100. Lizards were weighed at the start and the end of the test period and given neither food nor water.

Heart rate and oxygen consumption at rest, during maximum activity, and during recovery from exhaustive exercise were determined for five adult iguanas (two females and three males; $\bar{X}$ = 1252 g, range = 834-1722). Each lizard was tested on six consecutive days, starting at an air temperature of 15 C and increasing at 5 C increments to a maximum of 40 C. Experiments were conducted after 2100 on individuals which had received neither food nor water for two days prior to the first run. After each run the chamber air temperature was elevated five degrees for the next night's run. When not being tested, animals were permitted to move freely about the 1.4 by 2.5 m Environ-Room, kept on a 10L:14D cycle.

The lizard's exhaled air was trapped in a rectangular, black-painted Plexiglas mask fitted over the head. The mask had a neoprene apron glued to its open posterior end, which fitted over the lizard's anterior trunk and forelegs. Room air was sucked into the open posterior end of the apron, past the lizard's head, and out the front of the mask via Tygon tubing through columns of soda lime and Drierite, to remove carbon dioxide and water vapor, respectively. Flow rates ranged from 280 to 2440 cc/min. The gas then passed through a flowmeter, a pump, another flowmeter, and finally through a Beckman C-2 paramagnetic oxygen analyzer, located outside the Environ-Room. Gas flows were measured with rotameters calibrated with a Brooks Vol-U-Meter. The decrease in percent oxygen resulting from the lizard's respiration was recorded continuously, except during the exercise period, with a Honeywell Electronic 15 stripchart recorder. Lizards were kept in total darkness

during all oxygen consumption measurements. Oxygen consumption was calculated from oxygen content and flow rate data using the appropriate equation given by Depocas and Hart (1957).

For each run, a rectal YSI probe was inserted into the lizard's intestine. The animal was then fastened in a supine posture to a wooden jig, with its head resting inside the mask, taped to the jig. Oxygen consumption was monitored until a stable resting rate was achieved. The lizard was then removed from the jig and mask and exercised by hand manipulation for several minutes, sufficient to completely exhaust the animal. The lizard was immediately refitted into the mask and refastened to the jig. ECG needle leads were pushed beneath the skin of the shoulder and the base of the tail. Heart rate was measured every 4-10 minutes of the recovery period with a Physiograph Four A with high gain preamplifier (E and M Instrument Co.), located outside the Environ-Room. When oxygen consumption again fell to the resting rate, the lizard was manipulated by hand for another two minutes to get a maximum heart rate reading.

ECOLOGICAL ASPECTS OF THE THERMAL BIOLOGY OF *CYCLURA CARINATA*

Climate of Water Cay

The Caicos Islands are in the northern tropical zone, slightly below the Tropic of Cancer. They are also in the tropics under the Köppen System (Köppen 1923), since mean monthly shaded air temperature never falls below 18 C. Water Cay has a trade wind littoral climate, with fairly uniform high temperature and distinct wet and dry seasons.

Figure 1 summarizes the black body temperature measurements taken during three trips to Water Cay. *Cyclura* had to remain intermittently in the shade on sunny days during a large portion of its activity period or face lethal body temperatures due to radiant heat input. Adult lizards provided with some well timed overcast periods could theoretically survive in an exposed location all day in at least October to February. Yearly photoperiod varied by almost three hours, reflected in the difference in width of the heating curves for February vs. July.

Figure 2 illustrates the annual air temperature cycle near the two primary locations where *Cyclura* was observed. The range of mean shaded air temperature was only 4.5 C on Grand Turk. Of course, both daily and seasonal microclimatic extremes at ground level were greater. Gainesville, located in the subtropics, was too cold part of the year to support a *Cyclura* population. From the beginning of April until the end of September, penned Gainesville lizards ate readily and gained weight. Feeding was negligible during the other six months of the year.

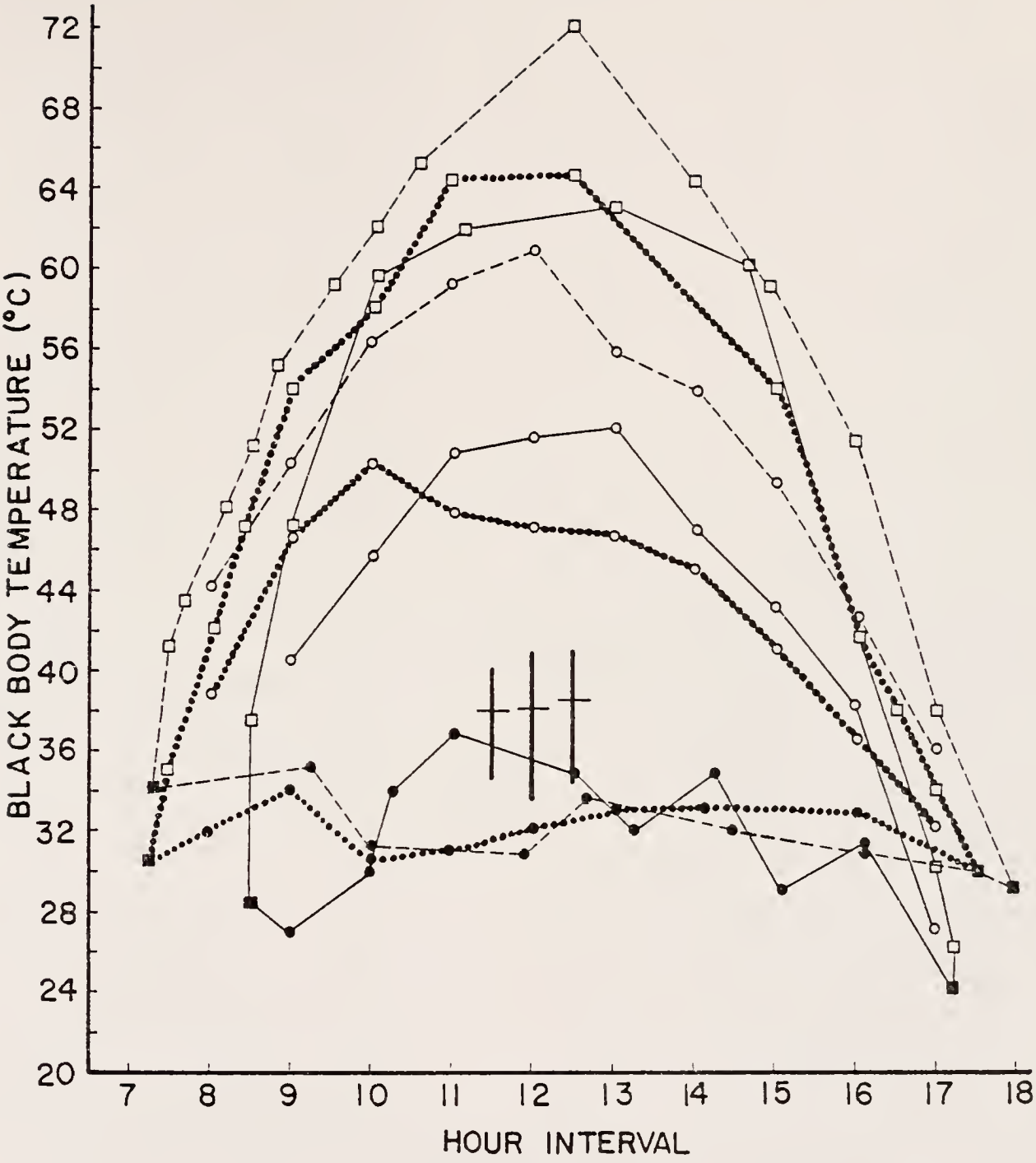


Figure 1. Black body temperatures in the field. February, June, and October measurements are represented by solid, dashed, and dotted lines, respectively. Maximum temperatures during the recording periods are represented by open squares, mean temperatures for the hourly intervals by open circles, and minimum temperatures by solid circles. All weather conditions encountered were included in the calculations. Horizontal lines are means and vertical lines are ranges of regulating phase T_b's of lizards at Site II for February, July, and October, respectively.

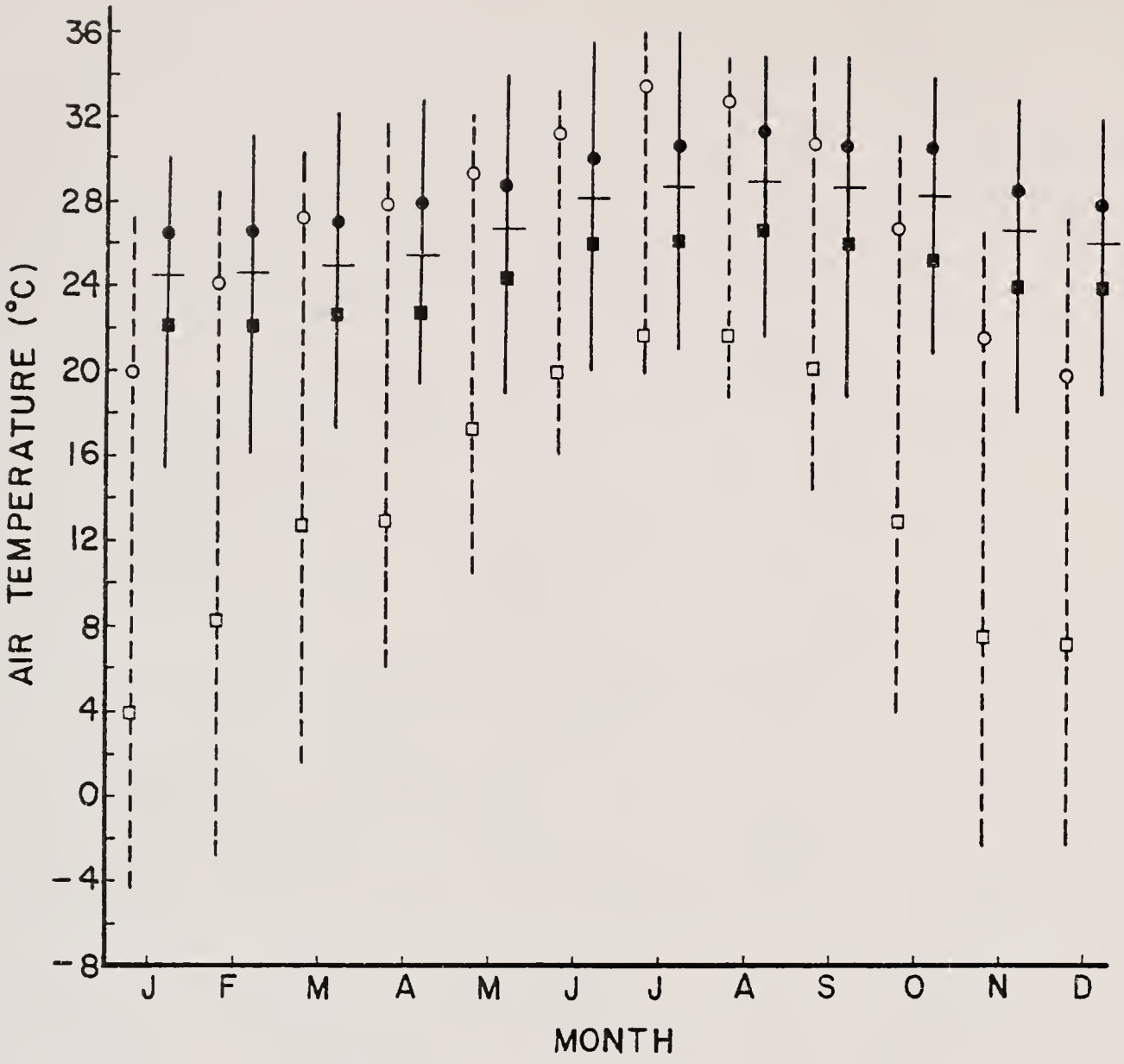


Figure 2. Air temperature in the shade at Gainesville, Florida (Agronomy Farm Weather Station; 29° 40' N, 82° 20' W; Prine 1977; and Grand Turk, British West Indies (Auxillary Air Field; 21° 26' N, 71° 8' W). Vertical lines extend from the maximum to the minimum recorded T_a each month (dashed line for the year 1976 at Gainesville, solid line for the years 1900-1968 at Grand Turk). Horizontal lines are mean monthly temperatures on Grand Turk. Circles and squares represent mean maximum and mean minimum air temperatures, respectively. Air temperatures were measured in a standard NOAA shelter (Stevenson screen) at a height of 1.5 m.

Special precautions had to be taken to prevent the lizards from freezing to death between November and February.

An easterly wind blew almost continually over the islands. The mean surface wind speed on Grand Turk was 24.6 km per hour (15.3 mph). Figure 3 illustrates the mean maximum July wind speeds on a road protected on the windward side by a limestone ridge and dense scrub at Site II. Wind speeds were greatest during the middle of the day, a typical pattern (Geiger 1957). Wind speed was greater at 50 cm than at 3 cm above the ground, also a typical pattern. Thus, lizards basking or feeding above the ground were usually cooled at a greater rate by forced convection than lizards on the ground. Wind speed was considerably higher facing the inlet between Water and Pine Cays just a few meters away. Since lizard burrows were common near the top of the ridge, some interesting wind related behavior was expected there, perhaps similar to the seeking out of minimal wind exposure at low T_b and maximum exposure at high T_b as seen in *Amblyrhynchus cristatus* of the Galapagos Islands (Bartholomew 1966, Bartholomew *et al.* 1976).

Rainfall was distinctly seasonal in the Caicos (Figure 4). Mean annual rainfall on Pine and Water Cays was probably slightly greater than on Grand Turk (597 mm or 23.5 inches). Four seasons characterize the western islands of the Caicos; a cool dry winter from January to March, a warm dry spring from March to May, a hot, increasingly wet summer from June to October, and a warm, wet autumn from October to December.

Water Cay was fairly humid (Table 1). Daily relative humidity decreased as air temperature increased, minimizing near midday. Of

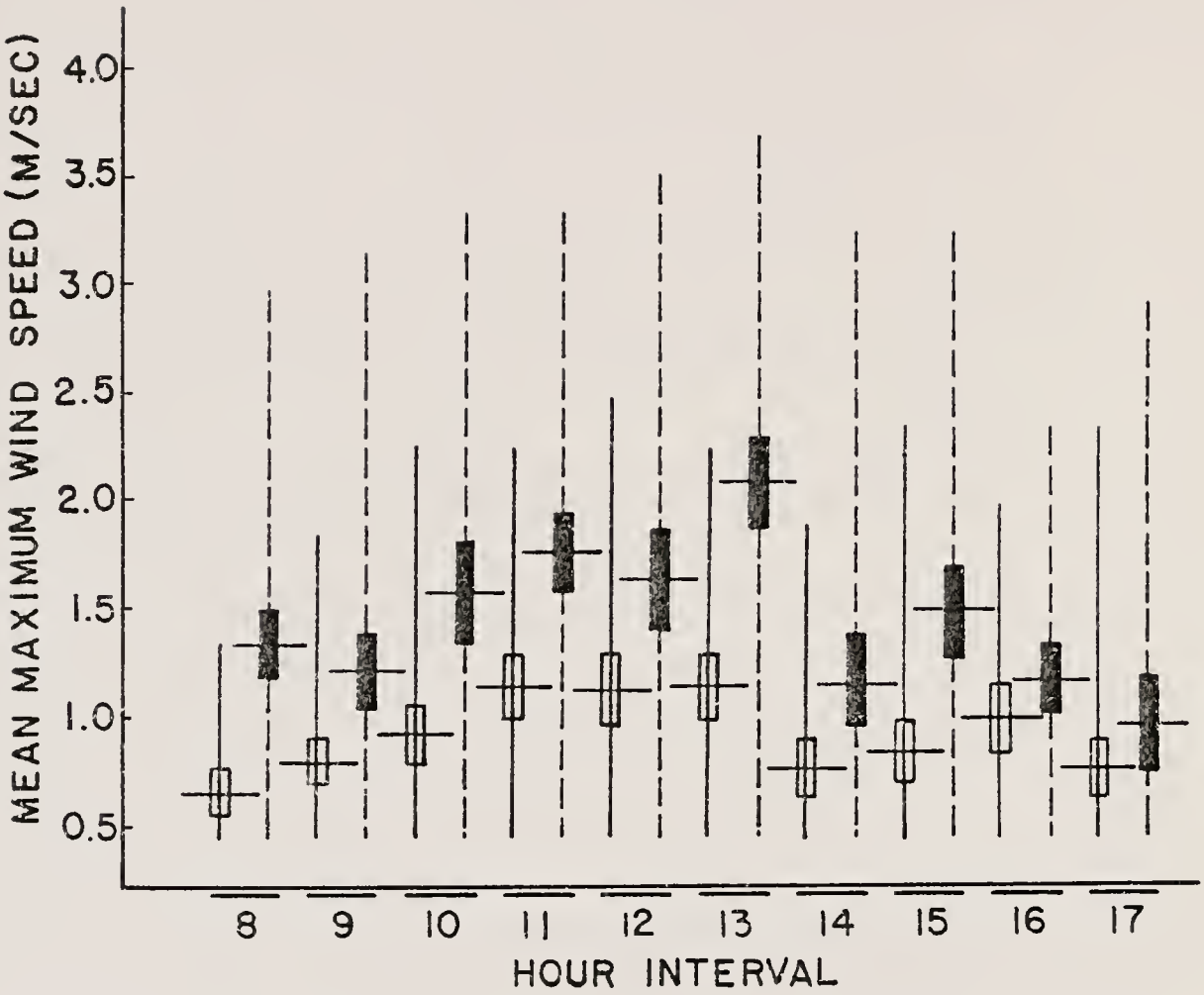


Figure 3. Mean maximum wind speed at Site II in July. Ten consecutive wind speed maxima were measured each hour for seven days at 3 cm (open rectangles) and 50 cm (solid rectangles) above the ground. Horizontal lines are means, vertical lines are ranges, and rectangles are plus and minus two SE of the mean.

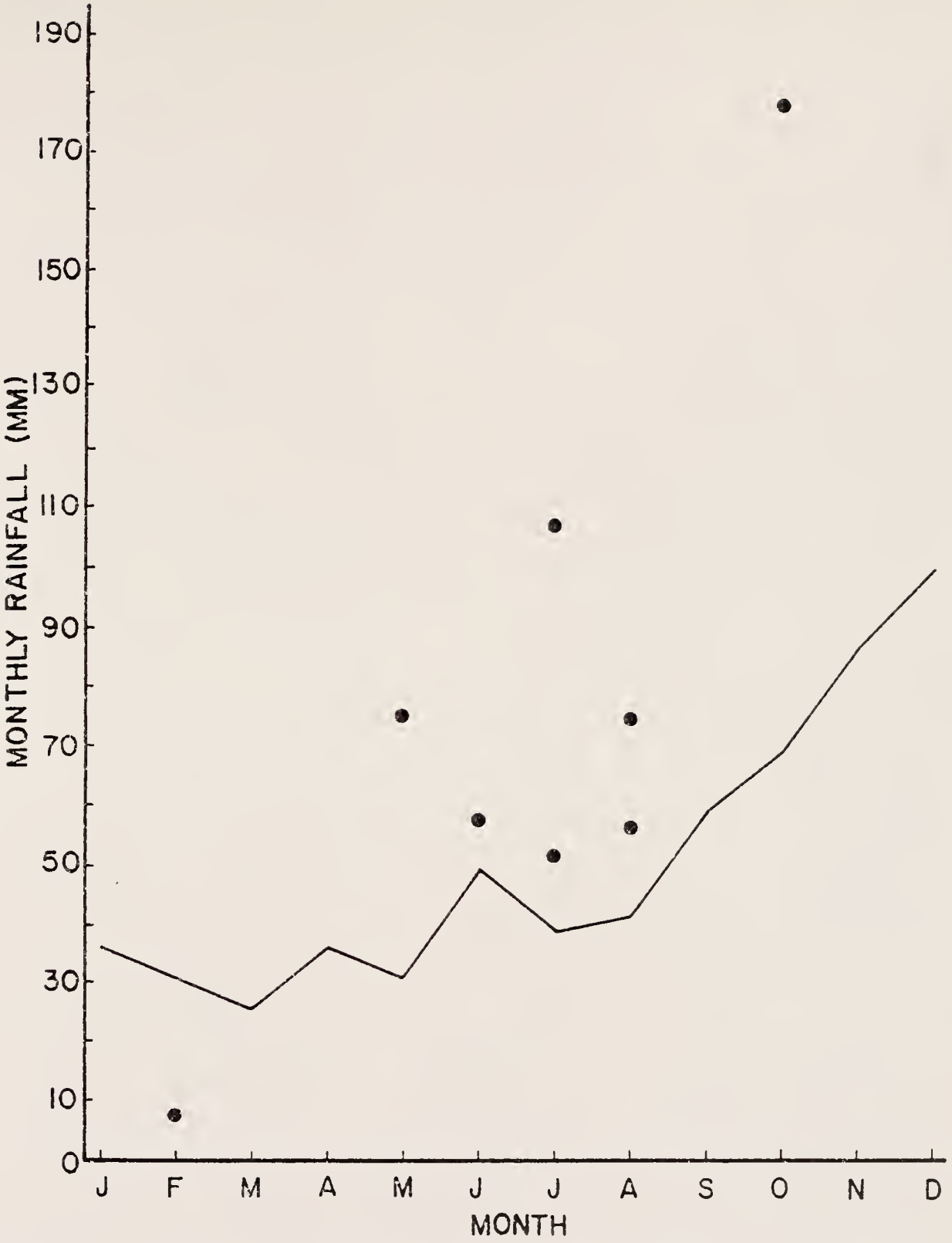


Figure 4. Monthly precipitation on Grand Turk, British West Indies. The line represents the mean monthly rainfall for the years 1900-1968. Total rainfall per month for several months on Pine Cay, Caicos Islands, are represented by dots.

Table 1. Daily variation in relative humidity. Measurements taken during hours of precipitation were not included. Data were collected at Site I (Jun) and Site II (Feb, Jul, Oct) on Water Cay.

HOUR INTERVAL	MEAN HOURLY RELATIVE HUMIDITY			
	FEB	JUN	JUL	OCT
	N=4	N=12	N=15	N=7 DAYS
0700-0759	-	75	74	86
0800-0859	78	74	71	77
0900-0959	67	69	64	69
1000-1059	66	62	64	64
1100-1159	66	59	61	62
1200-1259	60	59	64	62
1300-1359	61	64	63	59
1400-1459	62	61	64	64
1500-1559	66	61	65	66
1600-1659	70	67	71	70
1700-1759	73	72	71	78
MINIMUM DAILY READING	56	46	52	62
MAXIMUM DAILY READING	79	80	80	87
RANGE	23	34	28	25
MEAN MONTHLY RH	66.0	64.6	66.9	68.0
2SE	2.1	1.4	1.5	2.4

course, daily absolute humidity did not vary as much as relative humidity. Mean monthly relative humidity did not differ significantly between February, June, July, and October.

Diel Body Temperature Cycle of a Heliothermic Lizard

The body temperature cycle was divided into four phases by Wilson and Lee (1974). Some slight alterations were made for the following scheme (Figure 5).

1. Morning Heating Phase The lizard emerged from its burrow and heated rapidly in direct sunlight. *Cyclura* usually started its first feeding foray below the first maximum T_b, upon reaching the "normal activity range" (Cowles and Bogert 1944). Wilson and Lee's "basking phase" ends here. This term is confusing since basking did not cease when the first feeding foray began. Also, *Cyclura* was so wary during the June-July trip that it was very difficult to observe the start of the first foray unless I was sitting in a well positioned blind. Therefore, the first phase has been called the morning heating phase, ending at the first maximum T_b. This endpoint is obvious on a continuous T_b record.

2. Regulating Phase T_b fluctuated between a series of maxima and minima, staying within a fairly narrow range.

3. Burrow Cooling Phase It started at the lizard's evening submergence and ended during the night, when T_b had fallen to the 24 hour minimum. The decline in T_b followed a Newtonian cooling curve, with an ever decreasing rate of T_b decline as the stable deep burrow temperature was approached.

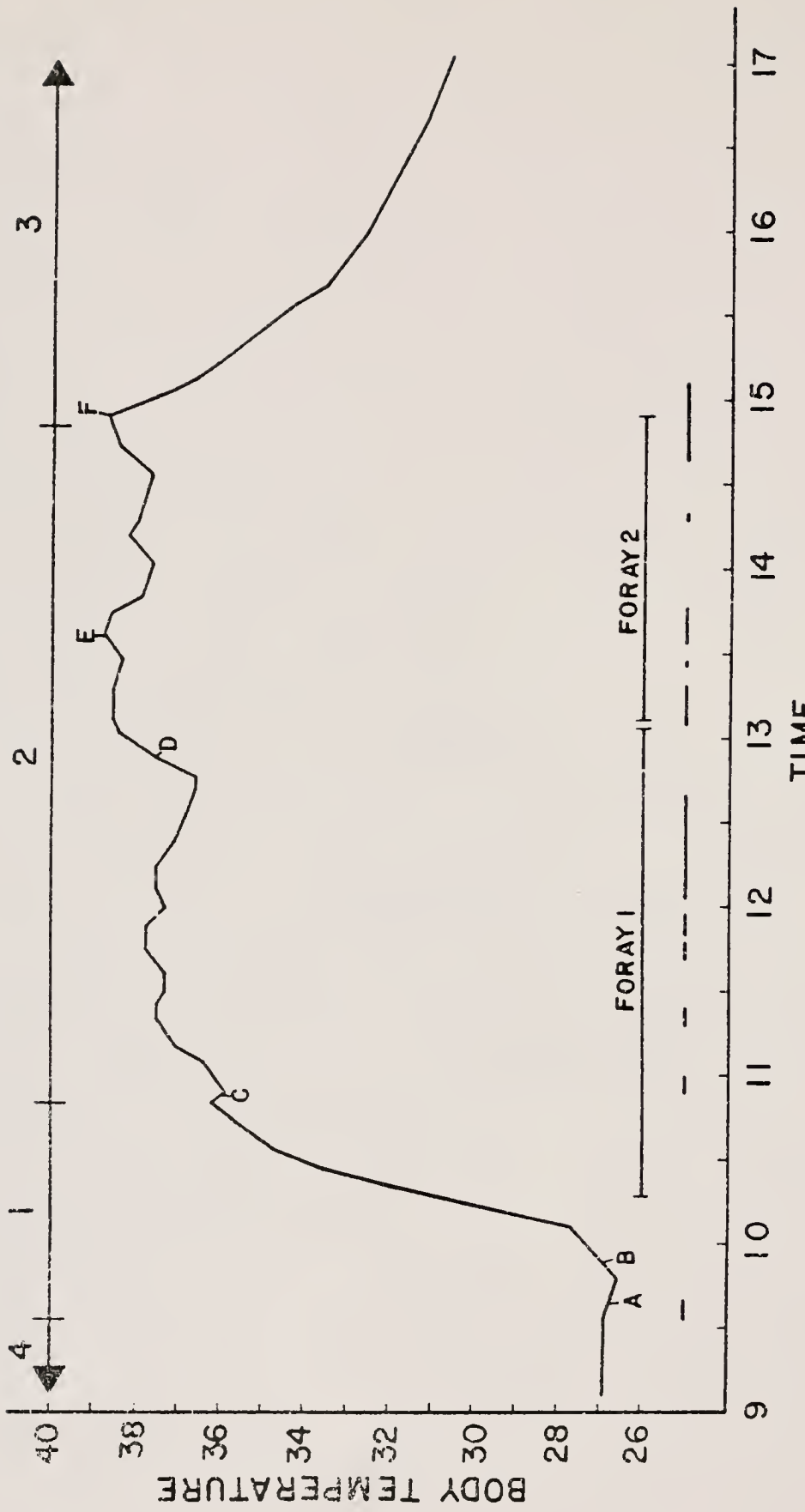


Figure 5. Body temperature record of Lizard 2 on February 10, 1976. The Arabic numerals at the top of the graph refer to the four phases of the T_b cycle. The broken line at the bottom indicates the periods when the sun was obscured by clouds. Capital letters refer to data points discussed in the text.

4. Stable T_b Phase The lowest T_b in the 24 hour cycle occurred just before emergence in two lizards larger than *Cyclura carinata*, the Lace Monitor, *Varanus varius* (Stebbins and Barwick 1968) and the Komodo Dragon, *Varanus komodoensis* (McNab and Auffenberg 1976). However, T_b stabilized considerably before emergence in *Cyclura*, necessitating a fourth descriptive phase. The term "inactive phase" used by Wilson and Lee would be confusing since *Cyclura* was also inactive in the burrow cooling phase.

A continuous body temperature record provides a substantial amount of information about a lizard. It was sometimes difficult to determine the exact time of emergence from the record, since deep burrow temperature was slightly greater than surface temperature early in the morning. The lizard in Figure 5 may have lost heat on the surface just after emergence (A) or near the burrow mouth prior to emergence (B). Slight differences in emergence T_b could sometimes be used to determine the burrow the lizard spent the night in, without having to locate the burrow the preceding night by following the increasing signal strength with the receiver. The time of submergence (F) is easily discerned in the February record. However, determination of submergence time from the summer records was commonly more difficult, since T_b often fell prior to submergence and at a rate not easily distinguished from the initial decline after submergence. Body temperature shifted abruptly upward as the overcast cleared temporarily at (D), a change maintained until submergence. Shifts of this sort were fairly common in the records.

Several further terms concerning lizard T_b need to be defined. All refer to measurements on a single individual taken during its

regulating phase. Unless otherwise specified, each T_b reading used in a calculation occurred during a period of sunshine or overcast (10 minutes or less) which did not cause a decline in T_b.

1. Mean Daily T_b Once the continuous record for a single day was plotted, the first and last maxima plus points at fifteen minute intervals, on the hour, were averaged.

2. Daily Minimum, Maximum T_b The lowest, highest T_b recorded for the day (C and E, respectively, in Figure 5).

3. Mean Daily Minimum, Maximum T_b An average of the daily minimum, maximum T_b for a specified number of days.

4. Mean of Daily T_b Minima, Maxima An average of all minima, maxima for one day.

5. Mean of T_b Minima, Maxima An average of all minima, maxima for a specified number of days.

Regulating Phase Body Temperature in the Field

Cyclura carinata is a stenothermal lizard during the regulating phase (Table 2). The mean of the regulating phase T_b ranges for all the monitoring days during clear weather was only 3.3 C (SD = 1.3, range = 0.7-6.4, N = 106 days). The frequency distribution of these T_b ranges was positively skewed toward greater stenothermality, with a median of 2.9 C and a modal class of 2.0-2.4 C.

Adults rarely went into their burrows at Sites I and II because of extremely high surface temperatures, although this may have been a common behavior in more sparsely vegetated areas. Free-ranging lizards prematurely submerged for the day on only 19 occasions during 129 individual monitoring days: 45 percent due to rain, 40 percent due to

Table 2. Summary of regulating phase body temperatures of lizards in the field. Data are arranged by season, field site, sex, increasing body weight, and individually by decreasing daily mean T_b, each line equaling one day's monitoring. Mean T_b's were calculated from the entire record, irrespective of weather conditions or lizard location. The letters (B) and (SU) signify that the lizard was in a burrow or the sun was obscured by clouds (sun under) when the minimum T_b was recorded, respectively. Lizards 2 and 3 were monitored in February and October.

LIZARD (FREE OR CAGED)	SEX	WEIGHT (G)	SITE	DATE	MEAN T_b	S.D. OF MEAN	DAILY MINIMUM T_b	DAILY MAXIMUM T_b	RANGE	LENGTH OF REGULATING PHASE (MIN)	% TIME SUN BEHIND CLOUDS	% TIME LIZARD IN BURROW
1(F)	F	1135	II	2-19-76	37.7	0.82	36.2	39.6	3.4	293	4	0
				17	37.5	1.85	33.4(B)	39.8	6.4	280	15	36
				18	36.8	1.38	34.0(B)	38.8	4.8	240	30	19
2(F)	M	1665	II	2-05-76	40.8	0.46	40.2	41.5	1.3	142	10	0
				6	38.6	0.72	36.0	39.2	3.2	288	14	0
				7	38.4	0.68	37.1	40.0	2.9	264	8	0
				12	38.3	0.52	37.0	39.2	2.2	315	0	0
				11	38.3	0.27	37.5	38.6	1.1	187	28	0
				9	38.0	1.40	34.7(SU)	40.0	5.3	332	8	0
				8	37.7	0.94	35.4	39.0	3.6	333	0	0
				10	37.6	0.79	35.9	38.8	2.9	244	41	0
3(F)	M	1775	II	2-12-76	40.0	0.60	38.1	41.0	2.9	427	0	0
				13	38.5	0.53	37.1	39.4	2.3	363	40	0
				11	38.2	0.50	37.0	39.2	2.2	288	20	0
				14	38.2	0.63	36.6	39.5	2.9	426	8	0
				15	38.1	0.61	37.0	39.2	2.2	327	19	0
				19	37.8	0.48	36.4	38.6	2.2	330	3	0
				17	37.4	0.79	35.6	38.5	2.9	505	38	0
				18	37.4	0.69	35.8	38.7	2.9	360	43	0
				20	36.0	1.81	32.6(SU)	38.6	6.0	313	63	0

Table 2. Continued.

LIZARD (FREE OR CAGED)	SEX	WEIGHT (G)	SITE	DATE	MEAN T_b	S.D. OF MEAN	DAILY MINIMUM T_b	DAILY MAXIMUM T_b	RANGE	LENGTH OF REGULATING PHASE (MIN)	% TIME SUN BEHIND CLOUDS	% TIME LIZARD IN BURROW
4(C)	F	645	I	6-10-74	40.8	2.03	37.6	43.8	6.2	419	30	NOT
				9	40.4	1.14	38.2	41.8	3.6	260	23	APPLICABLE
				8	40.3	1.63	37.4	42.6	5.2	288	7	"
				11	39.9	3.00	35.8	42.0	6.2	312	24	"
				7	39.1	0.93	37.1	41.0	3.9	360	0	"
5(C)	F	723	I	6-24-74	41.9	0.81	40.4	43.7	3.3	325	0	"
				25	41.5	0.42	40.7	42.5	1.8	501	0	"
				22	40.6	0.95	38.5	41.5	3.0	272	29	"
				26	40.6	0.58	39.3	41.7	2.4	481	3	"
				27	40.0	0.76	38.2	41.4	3.2	507	0	"
				28	39.3	0.96	37.2	41.4	4.2	525	10	"
				29	39.3	0.68	38.0	40.2	2.2	459	0	"
				7-01	35.3	3.79	28.6(B)	39.8	11.2	481	72	"
6(C)	F	815	I	6-17-74*	39.0	0.48	37.8	40.0	2.2	315	50	"
				9	38.8	1.29	37.2	40.8	3.6	291	29	"
				8	38.3	0.40	37.4	39.4	2.0	268	11	"
				18	38.3	4.18	33.9(SU)	41.3	7.4	242	42	"
				10	38.3	1.10	36.4	39.8	3.4	430	29	"
				7	37.6	1.29	35.7	39.8	4.1	407	2	"
				14	37.0	1.37	34.8	38.6	3.8	326	31	"
				11	36.5	1.36	34.9	37.8	2.9	315	24	"
7(C)	M	1290	I	6-24-74	40.7	0.63	39.4	41.9	2.5	325	0	"
				22	40.3	0.63	38.0	41.8	3.8	332	24	"
				29	38.7	0.96	36.3	40.8	4.5	465	0	"
				25	38.1	1.24	35.3	41.3	6.0	465	0	"
				26	38.1	1.01	35.7	39.7	4.0	488	3	"

Table 2. Continued.

LIZARD (FREE OR CAGED)	SEX	WEIGHT (G)	SITE	DATE	MEAN T_b	S.D. OF MEAN	DAILY MINIMUM T_b	DAILY MAXIMUM T_b	RANGE	LENGTH OF REGULATING PHASE (MIN)	% TIME SUN BEHIND CLOUDS	% TIME LIZARD IN BURROW
7(Continued)				27	38.0	1.16	36.0	40.1	4.1	507	0	NOT
				28	37.8	1.11	35.3	39.9	4.6	417	12	APPLICABLE
				7-01	35.0	3.22	29.3(B)	39.7	10.4	507	69	"
8(F)	F	675	I	6-26-74	41.9	0.44	40.7	42.9	2.2	420	0	0
				25	40.9	0.87	39.3	42.1	2.8	493	0	0
				14	40.6	0.97	37.7(SU)	42.1	4.4	321	21	0
				16	39.8	0.66	38.5	42.3	3.8	457	0	0
				24	39.8	0.46	38.4	40.6	2.2	360	7	0
				22	39.6	0.60	37.3	40.3	3.0	378	22	0
				17	39.6	1.38	36.7(SU)	42.1	5.4	393	51	0
				23	39.2	0.71	37.5	40.2	2.7	339	10	0
				18	38.4	1.93	30.3(SU)	40.5	10.2	300	34	0
				12	35.2	3.04	30.4(B)	40.9	10.5	429	0	43
				15	33.8	4.45	29.7(B)	42.1	12.4	330	45	170
9(F)	M	1450	I	6-29-74	42.4	0.37	41.6	43.3	1.7	490	0	0
				28	42.4	0.46	41.6	43.5	1.9	525	0	0
				17	42.3	0.39	41.5	43.0	1.5	390	54	0
				27	42.2	0.66	40.9	43.2	2.3	486	0	0
				24	41.7	0.42	40.8	42.6	1.8	378	7	0
				16	41.6	0.70	40.5	43.3	2.8	457	0	0
				23	41.0	0.48	39.9	41.6	1.7	351	10	0
				25	40.1	0.57	39.4	41.2	1.8	450	0	0
				7-02	40.0	1.05	38.1	42.5	4.4	510	14	0
				6-26	39.9	1.08	38.0	41.4	3.4	480	3	0
				7-01	39.2	0.51	38.1	39.9	1.8	267	47	0
				4	37.2	3.82	29.8(B)	40.9	11.1	455	26	17
				6-15	35.0	4.31	28.9(SU)	41.0	12.1	358	35	0

Table 2. Continued.

LIZARD (FREE OR CAGED)	SEX	WEIGHT (G)	SITE	DATE	MEAN T_b	S.D. OF MEAN	DAILY MINIMUM T_b	DAILY MAXIMUM T_b	RANGE	LENGTH OF REGULATING PHASE (MIN)	% TIME SUN BEHIND CLOUDS	% TIME LIZARD IN BURROW
10(F)	M	787	II	7-18-74	40.8	0.85	38.8	42.5	3.7	408	10	0
				13	39.9	1.79	36.9	42.9	6.0	500	0	0
				15	39.5	0.58	38.2	40.6	2.4	375	6	0
				12	38.6	1.07	37.1	40.8	3.7	486	6	0
				16	38.5	1.07	35.2(B)	40.6	5.4	384	2	9
				20	38.4	1.43	32.1(B)	40.2	8.1	450	19	8
				22	38.4	1.39	35.9	40.7	4.8	487	12	0
				21	38.1	1.21	35.3	40.2	4.9	435	5	0
				19	37.4	2.39	31.9(B)	40.6	8.7	431	0	20
				23	37.1	1.30	34.9(SU)	39.5	4.6	318	16	0
				11	36.9	1.60	33.3(B)	39.9	6.6	460	0	31
				17	34.4	3.30	30.1(SU)	38.9	8.8	405	62	0
11(F)	M	1598	II	7-09-74	41.4	0.87	39.0(SU)	42.9	3.9	396	35	0
				10	41.3	0.33	40.3	42.1	1.8	420	30	0
				11	40.8	0.36	40.1	41.5	1.4	481	0	0
				12	40.1	0.59	38.8	41.1	2.3	509	6	0
				18	38.9	0.66	37.4	40.1	2.7	480	8	0
				13	38.8	0.78	37.1	40.4	3.3	339	0	0
				6	38.5	0.25	38.2	38.9	0.7	178	20	0
				22	38.2	1.11	36.6	40.3	3.7	574	14	0
				15	38.1	0.66	33.7(SU)	39.6	5.9	550	27	0
				19	38.0	0.86	36.5	39.6	3.1	489	42	0
				20	38.0	0.64	36.9	39.3	2.4	470	24	0
				21	37.6	0.88	35.7	39.8	4.1	517	22	0
				23	37.1	1.49	33.8(SU)	39.6	5.8	575	26	0
				25	36.7	1.27	35.1	39.7	4.6	285	5	0
				7	36.2	1.11	34.1(SU)	38.4	4.3	234	100	0
				17	34.2	3.31	29.5(SU)	39.8	10.3	381	65	0
				16	28.0	0.10	28.0(B)	28.3	0.3	0	2	100

Table 2. Continued.

LIZARD (FREE OR CAGED)	SEX	WEIGHT (G)	SITE	DATE	MEAN T_b	S.D. OF MEAN	DAILY MINIMUM T_b	DAILY MAXIMUM T_b	RANGE	LENGTH OF REGULATING PHASE (MIN)	% TIME SUN BEHIND CLOUDS	% TIME LIZARD IN BURROW
12(F)	M	1420	I	8-28-76	39.7	0.28	39.4	40.2	0.8	114	0	0
				30	39.5	0.57	37.9	40.2	2.3	327	27	0
				29	36.3	2.31	32.2(B)	39.9	7.7	387	38	25
13(F)	M	950	III	9-03-76	39.3	0.69	38.2	40.4	2.2	195	35	0
				5	38.7	0.59	37.5	39.6	2.1	315	3	0
				4	37.8	1.14	35.2	39.4	4.2	213	62	0
				2	36.8	2.63	31.8(SU)	39.3	7.5	417	45	0
14(F)	M	1864	II	10-25-75	39.9	0.84	38.2	40.8	2.6	186	24	0
				21	39.7	0.36	38.5	40.7	2.2	300	18	0
				23	39.3	0.53	38.2	40.2	2.0	357	6	0
15(F)	M	1784	II	10-29-75	39.2	0.85	37.5	41.0	3.5	281	0	0
				28	39.2	0.82	37.3	40.7	3.4	313	31	0
				27	38.3	0.81	37.6	40.4	2.9	330	30	0
3(F)	M	1672	II	10-06-75	40.1	0.65	37.9	41.5	3.6	445	5	0
				5	38.6	3.30	31.0(B)	42.3	11.3	487	10	20
				7	38.2	1.44	35.0	40.6	5.6	345	30	0
				8	38.1	1.45	34.6(B)	40.4	5.8	380	0	12
				16	37.8	1.09	35.9	39.4	3.5	159	19	0
				21	37.7	0.95	36.2	39.7	3.5	255	13	0
				4	37.6	0.89	35.1	39.4	4.2	312	73	0
				20	37.5	1.29	35.2	39.7	4.5	270	22	0
				18	37.5	0.82	35.6	39.0	3.4	310	59	0
				19	37.3	0.76	34.5	38.3	3.8	354	5	0
				15	34.8	2.82	30.6(B)	39.2	8.6	285	21	49

Table 2. Continued.

LIZARD (FREE OR CAGED)	SEX	WEIGHT (G)	SITE	DATE	MEAN T_b	S.D. OF MEAN	DAILY MINIMUM T_b	DAILY MAXIMUM T_b	RANGE	LENGTH OF REGULATING PHASE (MIN)	% TIME SUN BEHIND CLOUDS	% TIME LIZARD IN BURROW
2(F)	M	1507	II	10-16-75	40.1	0.83	39.3	41.4	2.1	90	33	0
				19	39.5	0.37	38.5	40.1	1.6	308	6	0
				18	38.6	0.76	37.2	40.2	3.0	360	51	0

*Laid eggs in the cage during this day.

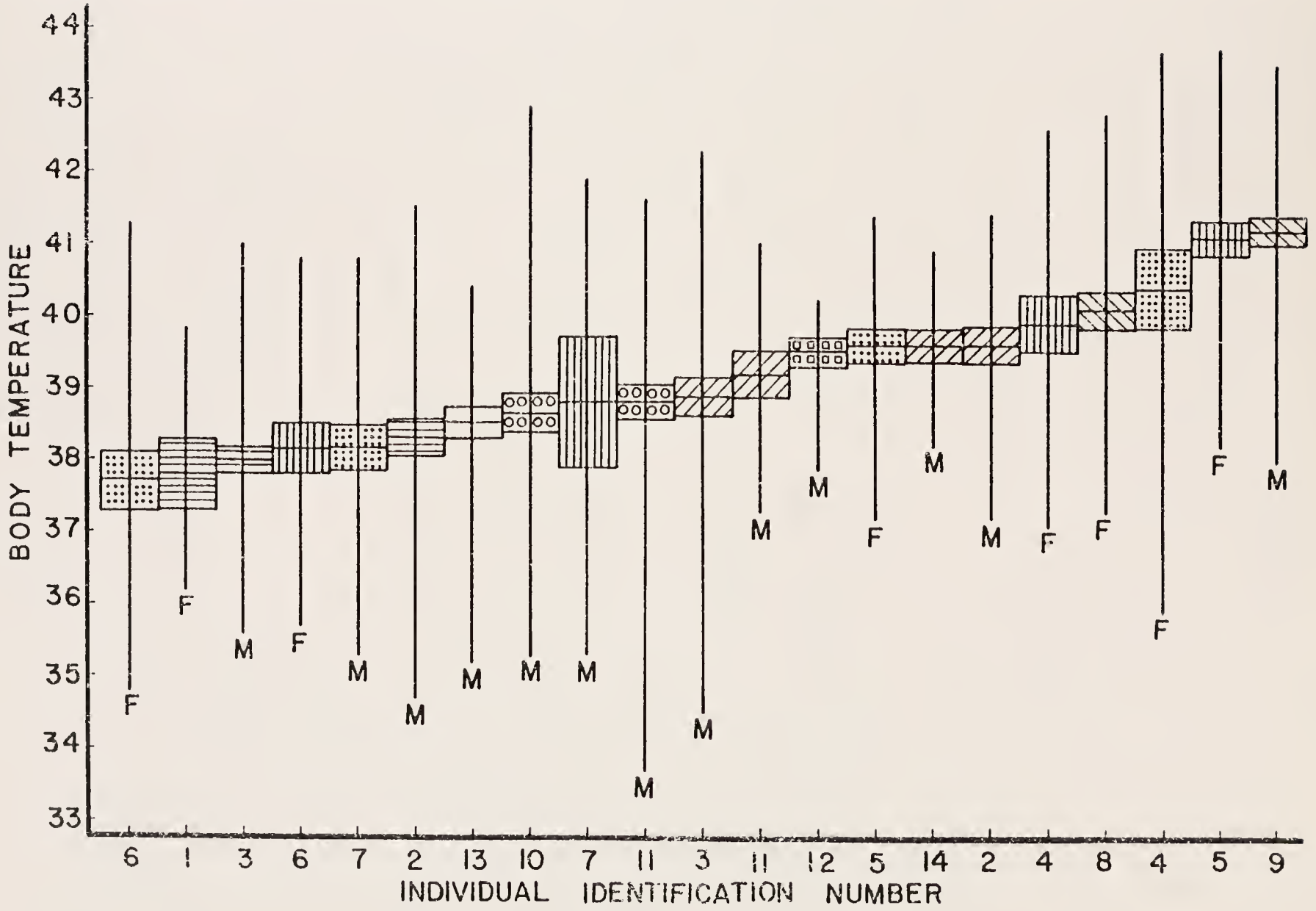
human disturbances, and 15 percent due to extreme cloudiness. Rates of cooling during burrow excavation and shade sitting were not consistently different. Thus, the cause of the cooling could not be determined by examination of the T_b record alone.

Figure 6 summarizes the regulating phase data for all the field lizards. The rise in mean T_b over the 3.5 C range was steady. Minimum T_b's fell into two groups having no correlation with increasing mean T_b's, one group above and one below 39 C mean T_b. This probably is of no significance. The correlation of maximum T_b with mean T_b was better. The lowest maximum T_b recorded was 1.6 C above the highest minimum. Thus, all T_b ranges of individuals overlapped somewhat, no matter what the sex, habitat type, or season of measurement.

The sample sizes were too small to determine conclusively whether or not mean T_b differed significantly with sex. Lizard 9, a dominant male, had a significantly higher T_b than Lizard 8 ($p \leq 0.05$), an adult female monitored simultaneously. However, two of three caged females in the simple habitat, Lizards 4 and 5, had significantly higher body temperatures than the caged male, Lizard 7. Mean T_b's were not significantly different in two free-ranging males and a female monitored at Site II in February.

Gravid females may have lower regulating phase T_b's than spent females and males. The gravid June female (Lizard 6) had the lowest mean T_b of all those monitored. The means were significantly higher ($p \leq 0.05$) for the other two caged females (Lizards 4 and 5) and the free-ranging female (Lizard 8) at Site I, all of which had probably recently laid eggs, since they actively defended their burrows against both encroaching males and females. However, Lizard 6's T_b was not

Figure 6. Summary of field body temperatures during the regulating phase. The lizards were monitored from 3 to 16 days. Mean regulating phase T_b was calculated from values taken at 15 minute intervals from the monitoring record. The number of days used to calculate each mean was variable and usually equal to the total monitoring time (Table 2). Periods of hyperthermia were included in calculation of the means, whereas periods of declining T_b due to overcast or burrow submergence were not. Vertical lines are ranges, horizontal lines are means, and rectangles are 99 percent confidence limits of the mean. Sex is indicated by an M or F. The four caged lizards in the complex habitat at Site I in June are represented by rectangles filled with vertical lines; the same four lizards in the simple habitat by dots; three free-ranging lizards in February at Site II by horizontal lines; two lizards in June at Site I by diagonal lines sloping downward to the right; two lizards in July at Site II by open circles; a single lizard in August at Site I by open squares; a single lizard in September on Fort George Island by an open rectangle; four lizards in October at Site II by diagonal lines sloping downward to the left.


BODY TEMPERATURE
44
43
42
41
40
39
38
37
36
35
34
33
F
F
M
F
M
M
M
M
M
M
M
F
M
F
M
F
F
F
M
6 1 3 6 7 2 13 10 7 11 3 11 12 5 14 2 4 8 4 5 9
INDIVIDUAL IDENTIFICATION NUMBER

significantly lower than the caged male, Lizard 7. On the single day Lizard 6's T_b was recorded after egg laying, the maximum was 0.5 C higher than the highest maximum of the seven monitoring days previous to laying. The highest mean T_b recorded was on the day she laid her eggs, but the mean was not significantly higher than the next two highest means recorded prior to laying. The differences probably would have been significant had not the day of laying been overcast 50 percent of the time.

Temporary Hyperthermia and Hypothermia

All eleven iguanas monitored in the field passed through a period of hyperthermia soon after release (Figure 7 and Table 3). T_b then declined to a more stable, presumably normal range. The T_b decline was either rather rapid as for Lizard 3 or more gradual as for Lizards 8 and 11. The extent of the hyperthermic response, as measured by the sum of the ranges of the maximum daily T_b and the mean daily T_b's between the hyperthermic peak day and the return to normalcy, was usually slightly greater in coelomically than enterically implanted lizards. However, the response may vary with season as well as with transmitter location. The summer animals were probably suffering from a bacterial infection resulting from transmitter implantations (see Vaughn *et al.* 1974, Kluger *et al.* 1975, and Bernheim and Kluger 1976a, b for related laboratory studies). The second T_b rise observed in Lizards 8 and 9 may have been due to reinfection of the wound or a secondary response to a chronic infection. In the latter case it may be that lizards could not tolerate a high T_b for more than a few days even though infectious agents were still present (Cowles and

Figure 7. Lizard hyperthermia and hypothermia during the regulating phase. Lines connect T_b maxima, omitting those during periods of heavy overcast (open circles). Open squares are daily T_b means. Lizard 11 was prevented from emerging on Day 3 by a land crab (*Cardisoma guanahumi*) ensconced for a single day just inside the burrow mouth. The transmitter was in the gut of Lizard 3 and in the coeloms of Lizards 8 and 11.

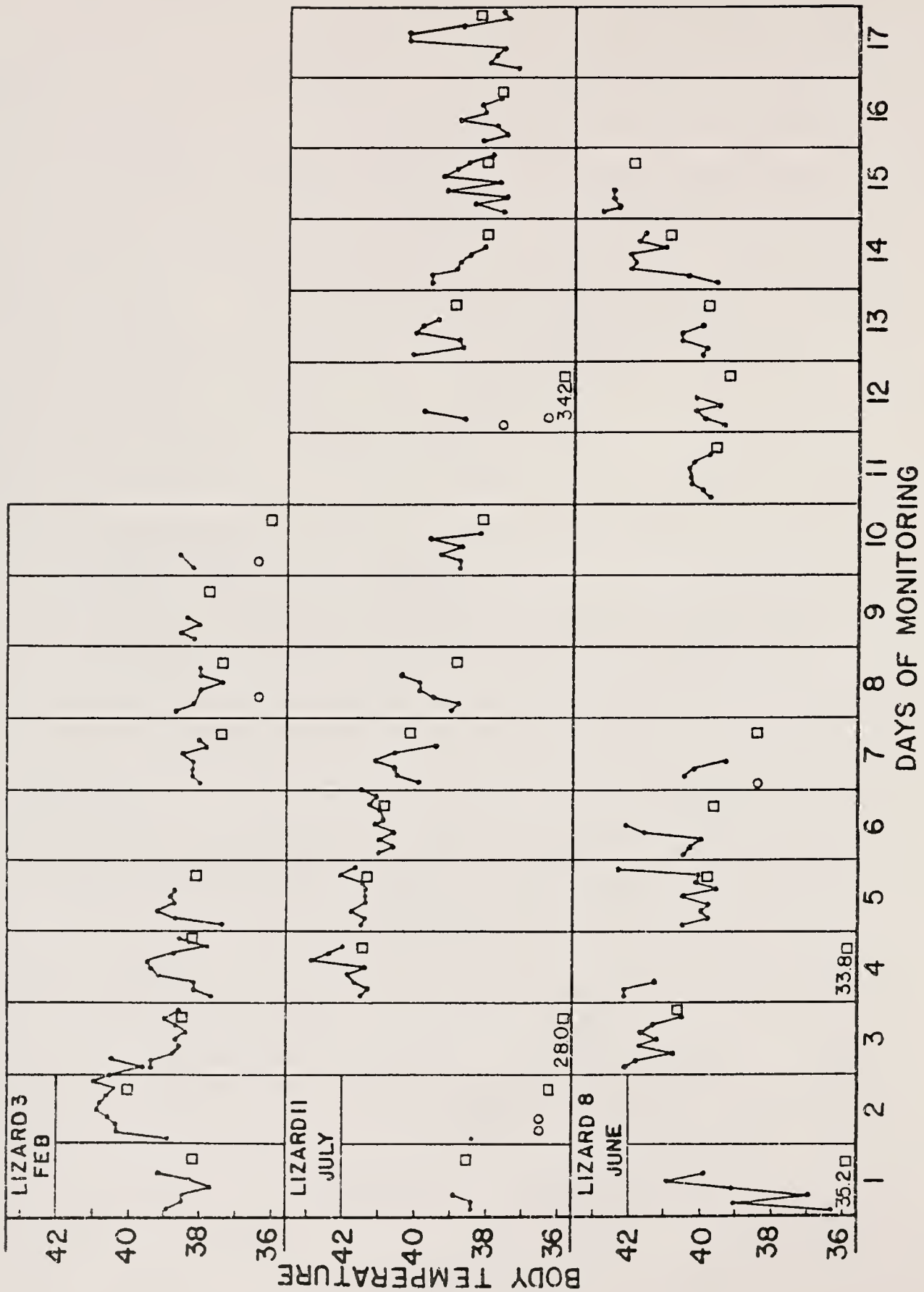

LIZARD 3
FEB
LIZARD 11
JULY
LIZARD 8
JUNE
BODY TEMPERATURE
DAYS OF MONITORING
42
40
38
36
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
35.2
28.0
33.8
34.2

Table 3. Hyperthermia in *Cyclura carinata* in the field. The ease of graphically distinguishing a T_b peak and a recovery from hyperthermia was classified as high, medium, or low. The maximum T_b was the highest body temperature recorded for a lizard. The low maximum T_b was the lowest maximum recorded on the day recovery was complete or before a second rise in T_b occurred (Lizards 8 and 9).

LIZARD	2	3	4	5	6	7	8	9	10	11	3	MEAN	S.D.
MONTH	FEB	FEB	JUNE	JUNE	JUNE	JUNE	JUNE	JUNE	JULY	JULY	OCT		
LOCATION OF TRANSMITTER	GUT	GUT	COELOM	COELOM	COELOM	COELOM	COELOM	COELOM	COELOM	COELOM	GUT		
CAGED OR FREE RANGING LIZARD	F	F	C	C	C	C	F	F	F	F	F		
DAYS LIZARD MONITORED	8	10	6	11	13	11	15	12	13	20	19		
CLARITY OF T_B TREND	MEDIUM	MEDIUM	HIGH	HIGH	LOW	HIGH	HIGH	HIGH	HIGH	HIGH	MEDIUM		
MAXIMUM T_B	41.5	41.0	43.8	43.7	39.9	41.9	42.1 42.9	42.6 43.5	42.9	42.9	42.3	42.3	1.2
DAY OF MAXIMUM T_B	1	2	5	4	1	4	3/15	2/6	3	4	3		
HOURS AFTER RELEASE T_B MAXIMUM RECORDED	4	28	100	75	4	72	49/339	25/125	55	73	48	48	31
LOW DAILY MAXIMUM T_B	37.6	37.4	---	38.7	37.5	36.3	39.4	38.7	35.9	37.8	37.6	37.7	1.1
DAY OF LOW DAILY MAXIMUM T_B	5	8	---	9	6	8	11	4	13	10	6		
TIME OF T_B MAX - TIME OF LOW T_B MAX (HOURS)	91	145	---	117	117	91	216/73	48/50	235	140	72	116	60
RANGE OF DAILY MAXIMUM T_B'S	3.9	3.6	---	5.0	2.4	5.6	2.7/3.5	3.9/4.8	7.0	5.1	4.7	4.4	1.3

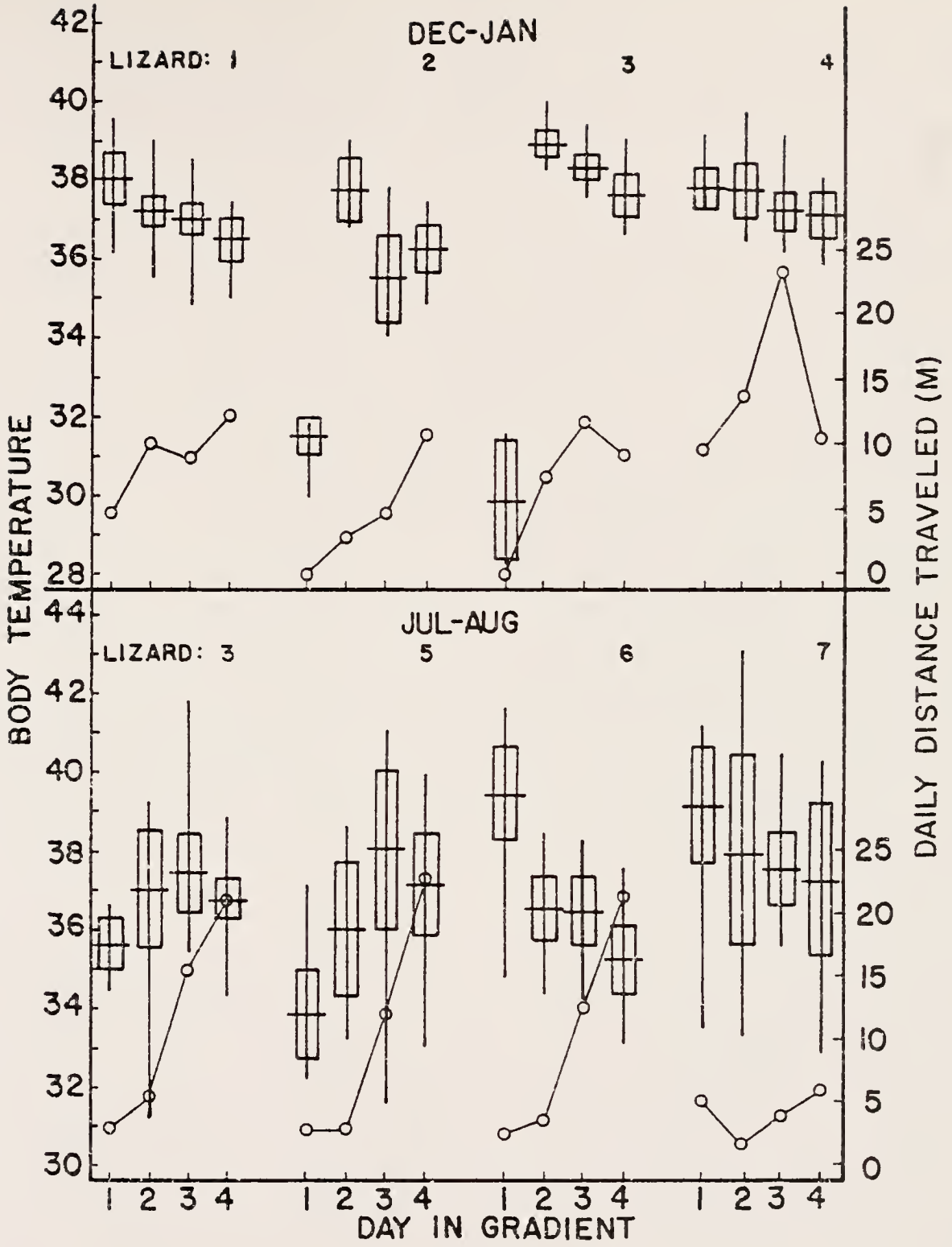
Table 3. Continued.

LIZARD	2	3	4	5	6	7	8	9	10	11	3	MEAN	S.D.
MEAN T_B ON DAY OF MAXIMUM T_B	40.8	40.0	40.8	41.9	38.8	40.7	40.6 41.9	41.7 42.4	39.9	41.4	38.6	40.7	1.2
MEAN T_B ON DAY OF LOW DAILY MAXIMUM T_B	38.0	37.4	---	39.3	36.5	38.0	39.2	39.9	37.1	38.1	38.1	38.2	1.1
RANGE OF MEAN	2.8	2.6	---	2.6	2.3	2.7	1.4/2.7	1.8/2.5	2.8	3.3	0.5	2.3	0.8

and Burleson 1944, Licht 1965b, Licht and Basu 1967, Kluger *et al.* 1975). The body cavity internal to the wound sites and surrounding the transmitter suppurated only slightly or not at all at the time transmitters were removed. The mean time between release and the maximum hyperthermic response was 2.4 days in summer *Cyclura* and 1-2 days in *Dipsosaurus* injected with live *Aeromonas* bacteria (Bernheim and Kluger 1976a). Recovery was complete in *Dipsosaurus* by the sixth day after injection and, on the average, by the seventh day after the operation in summer *Cyclura*. These similarities may signify that similar disruptions were in force in the brain thermoregulatory centers of both species. Hyperthermia in enterically implanted lizards may have been a feeding response to a transmitter meal or, somehow, a reaction to handling or the use of halothane. The lizard with the weakest response was Number 6, the gravid caged female. Embryonic development in *Cyclura carinata* begins within the female's body and continues after nesting at burrow temperatures of 28-29 C (Iverson 1979). Regulating phase T_b's in the range of nongravid lizards may be fatal to developing embryos in *Cyclura*, as they are in *Iguana iguana* (Licht and Moberly 1965). Thus, the hyperthermic response to bacterial infection may have been counterbalanced somewhat by a hypothermic response to gravidity.

Hyperthermia also occurred in the laboratory thermal gradient (Figure 8). The high daily mean T_b was significantly greater ($p \leq 0.05$) than the low in six of eight animals. The hyperthermic responses in the field and gradient were fairly similar; that is, a latent period of variable duration was followed by a maximum T_b and a decline. High mean T_b occurred in three species of *Phrynosoma* when first housed in

Figure 8. Patterns of regulating phase body temperature and distance traveled in *Cyclura carinata* in a laboratory thermal gradient. Data are presented for eight lizards, each monitored for four consecutive days. Lizard 3 was included in both samples. Horizontal lines are T_b means, vertical lines are ranges, and open rectangles are plus and minus two standard errors of the mean. The total distance each lizard walked (open circles) was measured during the full eight hour photophase.


DEC-JAN
LIZARD: 1
2
3
4
JUL-AUG
LIZARD: 3
5
6
7
BODY TEMPERATURE
DAILY DISTANCE TRAVELED (M)
DAY IN GRADIENT
42
40
38
36
34
32
30
28
44
25
20
15
10
5
0
1 2 3 4

terraria (Heath 1965) and in *Anolis carolinensis* when first introduced into a thermal gradient (Licht 1968). The authors believed the hyperthermia, which ceased after two days, was due to lizard inexperience in new surroundings. Learning the new thermal environment resulted in a decline in T_b to the preferred level. The same explanation probably applies to *Cyclura*. Four of eight lizards did not move voluntarily during the first day. Two of the lizards were located under the heat lamps when the photophase began. It was thought best to push them toward the cool end of the gradient when they began to pant. The steady increase in walking distance per day corresponded in part to learning how to maintain preferred T_b by shuttling.

The hyperthermic response, as measured by the difference between the maximum mean daily T_b minus the mean preferred T_b, is similar in the iguanid lizards studied to date: 1) 2.0 C in *Anolis carolinensis* by the third day in a thermal gradient (Licht 1968), 2) 2.3 C in field monitored and 2.2 C in gradient monitored *Cyclura carinata*, 3) 3.7 C in *Dipsosaurus dorsalis* on the second day after injection of dead *Aeromonas hydrophila* (Bernheim and Kluger 1976a), and 4) 2.9 C in *Phrynosoma* by the third day in a thermal gradient (Heath 1965). One explanation for the similarity in the responses is the constancy of the small temperature gap between the preferred T_b and the CTM in these lizards.

Voluntary hypothermia during the regulating phase was a rare event, observed in only two free-ranging summer lizards (8 and 10) on the day of their release. Lizard 8 never ventured further than a meter from its burrow the first day, retreating six times to the burrow for lengthy cooling periods (Figure 9). As T_b maxima increased, T_b minima increased also, resulting in a series of ascending peaks ending with the highest

Figure 9. Hypothermia in a free-ranging lizard. Lizard 8 was in its burrow (solid line) or lay partially exposed in the sandy depression in front of its burrow mouth (dotted line) for a considerable part of its first day after release.

41
39
37
35
33
31
29
BODY TEMPERATURE
RELEASE
830
930
1030
1130
1230
1330
1430
1530
1630
TIME

peak late in the afternoon. The same pattern was observed in only 2 of 51 thermal gradient records. Hypothermia in newly released field lizards may have been due to a temporarily heightened thermal sensitivity due to cooling to 3-12 C during the implantation operation the previous night.

The Relationship of Pertinent Environmental Variables to Regulating Phase Body Temperatures

Season

Table 4 summarizes the environmental temperature data accumulated for Site II. Mean black body temperature was not significantly different in February and October. The mean range was only 3.1 C between February, nearly the coldest month, and July, nearly the warmest. The mean differences between months for the other three temperature measures in the table were significant. The ranking was also consistent. The February-July mean temperature difference increased from 4.2 C for sun exposed sand and 4.7 C for shaded sand to 6.5 C for shaded air. Although the monthly percentages of time that clouds obscured the sun did not differ significantly, the thickness of the cloud cover and the percentage of the sky in overcast were greater during the rainy season in October than in February and July.

Mean monthly T_b did not correlate directly with changing monthly environmental temperature. Mean T_b at Site II was significantly higher in October than in February and July ($p \leq 0.01$, student's t test) and mean T_b's in February and July did not differ significantly from each other (Table 5). The seasonal variation in mean T_b was probably only slightly greater than 0.5 C (July minus February mean). The significant

Table 4. A seasonal comparison of some environmental variables at Site II on Water Cay. The data were collected at approximately hourly intervals from 0900 to 1700. Values are for a variety of weather conditions in February (15 days), July (16 days), and October (16 days).

	N	$\bar{X}$	$\bar{X}$+2SE	$\bar{X}$-2SE	HIGH	LOW
BLACK BODY TEMPERATURE						
October	191	44.1	45.4	42.8	64.4	27.0
February	109	44.2	46.1	42.3	63.0	24.1
July	181	47.2	48.8	45.6	67.4	28.3
SUN EXPOSED SAND TEMPERATURE						
February	101	33.4	34.9	31.9	>52.0	23.7
October	190	35.8	36.7	34.9	>52.0	25.1
July	177	37.6	38.5	36.7	>52.0	26.8
SHADED SAND TEMPERATURE						
February	109	26.3	26.9	25.7	36.3	21.4
October	192	29.1	29.5	28.7	39.6	25.1
July	182	31.0	31.3	30.7	35.5	26.5
SHADED AIR TEMPERATURE (HEIGHT 6 CM)						
February	109	26.3	26.7	25.9	32.6	22.1
October	193	30.5	30.9	30.1	38.1	24.2
July	181	32.8	33.1	32.5	37.2	27.8
PERCENT OF TIME SUN OBSCURED BY CLOUDS						
February	15	21.5	31.2	11.8	63	0
October	16	22.1	32.3	12.3	73	0
July	16	24.2	37.5	10.9	100	0
	N	TOTAL (mm)				
PRECIPITATION						
February	15	5				
July	16	36				
October	16	83				

Table 5. Seasonal changes in regulating phase body temperature in the field and in the laboratory thermal gradient. Only periods when the sun was not obscured by clouds were included in the field calculations. Only third and fourth day monitoring records were used in the calculation of mean T_b's for gradient lizards. Values were taken from the T_b records at 15 minute intervals. All lizards were non-hyperthermic.

MONTH	DAYS	FEMALES/ MALES	SITE	N	$\bar{X}$ T_b	$\bar{X}$+2SE	$\bar{X}$-2SE	SD	LOW	HIGH
				FREE-RANGING LIZARDS						
February	13	0/2	II	280	38.0	38.1	37.9	0.82	34.7	40.0
June	9	1/1	I	231	39.7	39.8	39.6	0.89	37.3	42.5
July	13	0/2	II	365	38.1	38.2	38.0	1.24	33.7	40.7
October	13	9/3	II	268	38.5	38.7	38.3	1.25	34.5	41.0
				THERMAL GRADIENT LIZARDS						
July-Aug	8	2/2		222	36.9	37.1	36.7	1.86	31.6	41.8
December-Jan.	8	2/2		174	37.1	37.3	36.9	1.08	34.0	39.3

difference between June and July T_b means was probably due to the difference in the amount of vegetation at Sites I and II. The variance of mean T_b in February was significantly lower ($p \leq 0.01$) than in July and October. The winter variance was lower primarily in the upper portion of the T_b range (Figure 10). Lizards had been acclimatized to the more thermally variable Gainesville climate before testing in the thermal gradient (Table 5). Yet, summer and winter sample T_b means did not differ significantly on any of the first four days in the gradient. As in the Caicos, the variance of the mean T_b for winter animals was significantly less than for summer animals ($p \leq 0.01$) and the lower winter variance was more evident at high T_b (Figure 10). Thus, acclimatization to low environmental temperatures in *Cyclura* appears to involve an increased avoidance of high and low regulating phase T_b's without change in mean T_b.

Mean T_b was significantly lower for *Cyclura* monitored in the gradient than in the field (Table 5). The July-August gradient mean was 2.8 C lower than the June field mean and 1.2 C lower than the July field mean. The difference was only 0.9 C for the winter field and gradient samples. In Figure 11 mean field T_b's of active lizards have been plotted against mean gradient T_b's for lizard species from several different families. Mean gradient T_b's are nearly always lower than mean field T_b's above a mean field T_b of 37 C. Allowing T_b to rise above the preferred gradient T_b is probably adaptive in diurnal heliotherms temporarily living in hot environments, such as *Cyclura* in summer, since morning and afternoon activity periods are thus lengthened (DeWitt 1967, Licht *et al.* 1966).

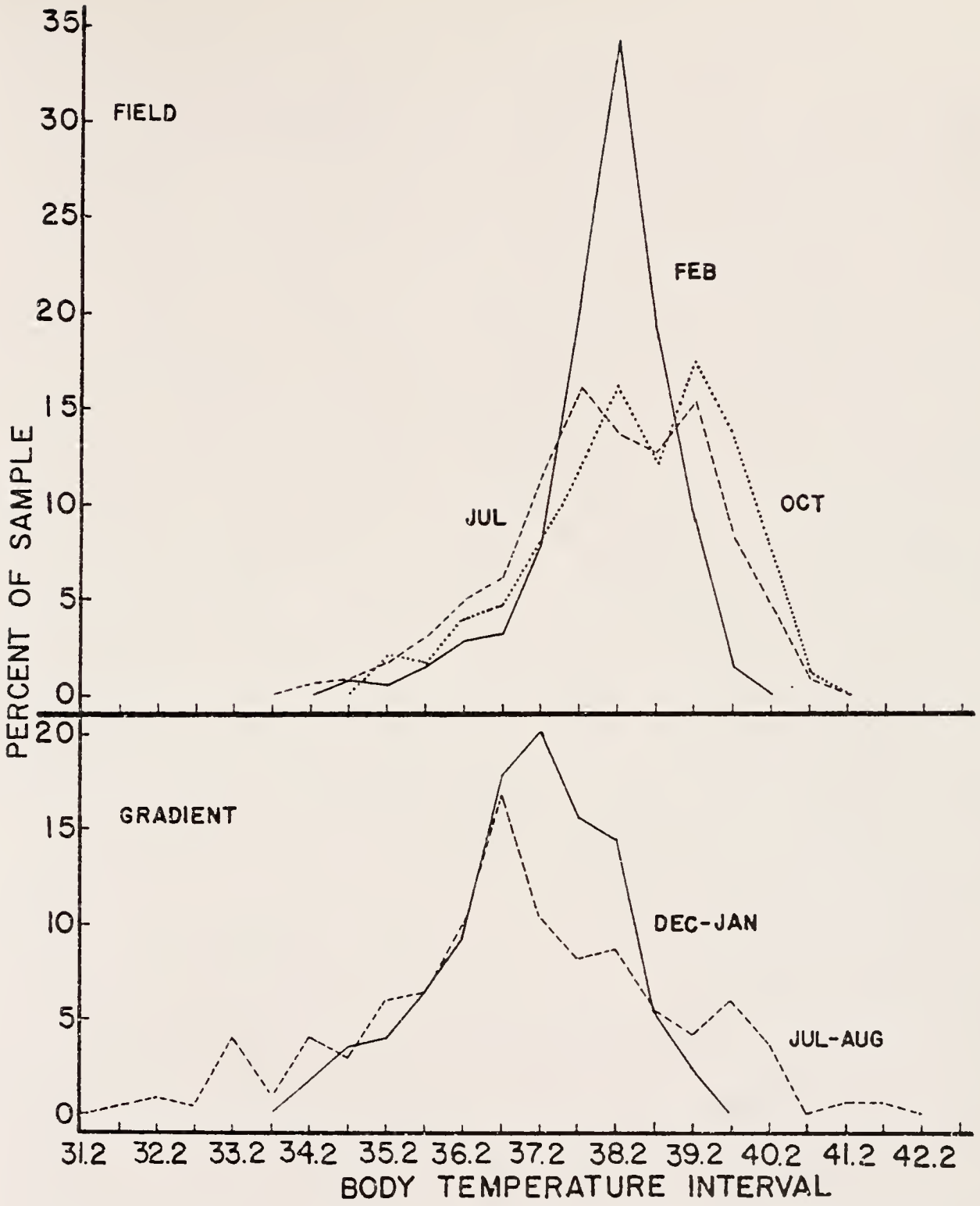


Figure 10. Seasonal change in *Cyclura* regulating phase body temperature in the Caicos and Gainesville, Florida. The February and July field distributions and the October field distributions are for two and three nonhyperthermic free-ranging male lizards, respectively. Each month's field sample consisted of a total of 13 monitoring days. The two thermal gradient distributions consisted of third and fourth day results for two males and two females.

There are at least three other reasons why lizards commonly have higher field T_b's than gradient T_b's. First, Regal (1971) found that a dominant *Klauberina riversiana* provided with a subdominant lizard in the same gradient box maintained a higher T_b than the same dominant lizard monitored separately. Since gradient lizards are usually tested singly, T_b's may be lower due to missing social interaction present in the field. Secondly, field T_b's measured by mercury thermometer rather than telemetry, as was the case for practically all the points in Figure 11, may be biased to those lizards in full sun and plain view as opposed to sequestered individuals in deeply shaded surface areas (McGinnis and Dickson 1967). Thirdly, lizards are commonly not fed while in the thermal gradient, although reptiles often have elevated active temperatures after feeding: lizards (Cogger 1974), snakes (Regal 1966), and turtles (Gatten 1974c).

The single anguid plotted in Figure 11, *Gerrhonotus multicarinatus*, which has such a low field temperature mean compared to its gradient mean, is probably forced to be eurythermal due to its habitat choice. It is a secretive, ground dwelling lizard living amongst shaded vegetation. The lizard does occasionally bask, reaching a voluntary maximum of approximately 35.7 C, considerably higher than the mean for active lizards (Cunningham 1966). The field T_b's for the five gekkonids in the figure were measured while the animals were in their diurnal retreats. Even though their T_b's during nocturnal activity must necessarily conform to air and substrate temperatures, gekkonids in their diurnal retreats commonly seek out T_b's as high or higher than their preferred gradient T_b's. The high diurnal T_b's may be necessary for digestion of food collected during the night (Bustard 1970, Pianka and Pianka 1976).

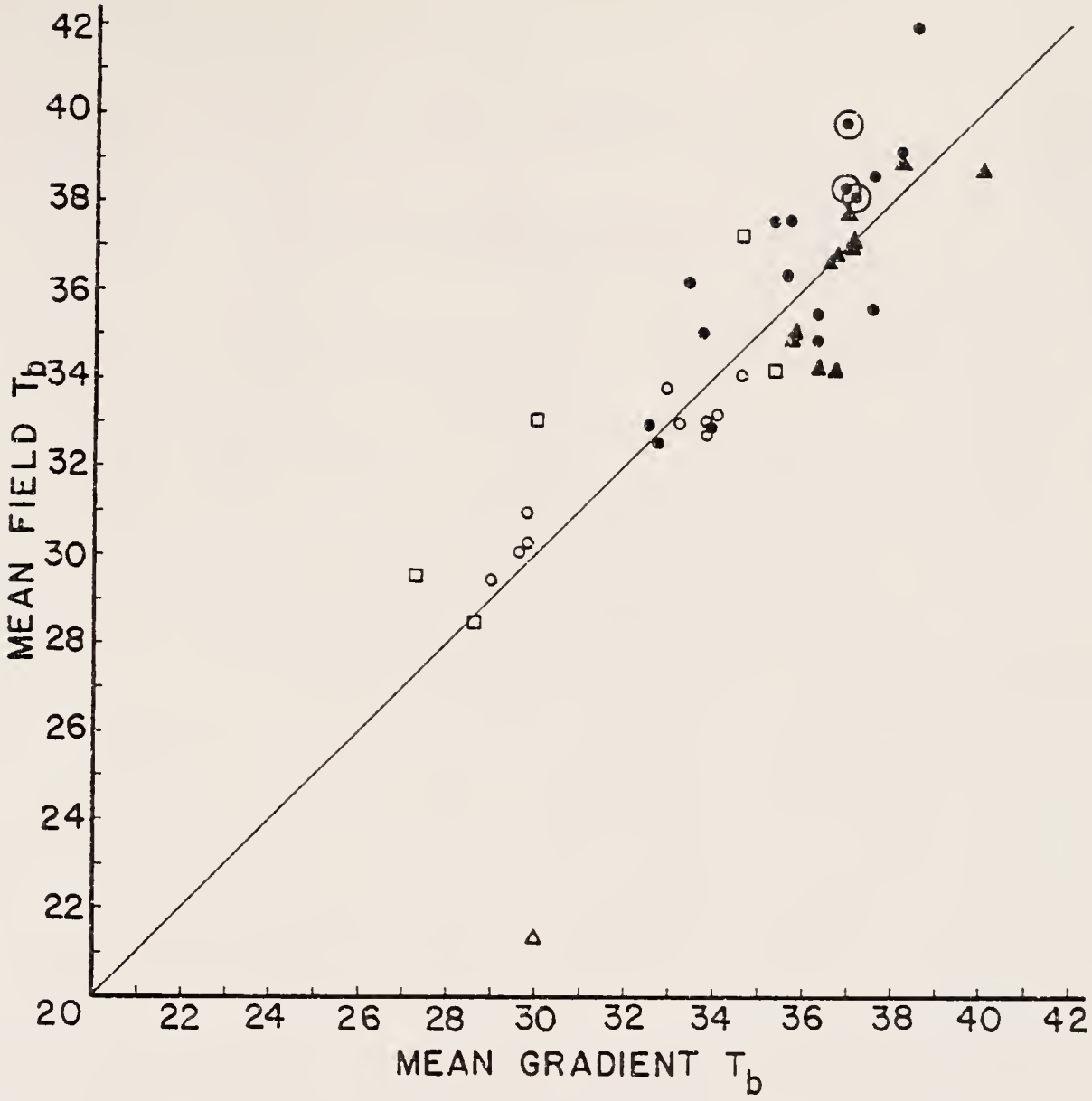


Figure 11. Relationship of mean body temperatures in the field and the thermal gradient for active lizards from several families. Solid triangles represent agamids, open triangle, anguid; open squares; gekkonids; solid circles, iguanids; circles enclosing dots, *Cyclura* at Site I in June and Site II in July vs. the summer gradient mean and at Site II in February vs. the winter gradient mean; open circles, scincids. Data were taken from several sources: Bradshaw and Main 1966, Brattstrom 1965, Cowles and Bogert 1944, Cunningham 1966, DeWitt 1967, Fitch 1954, Fitzpatrick *et al.* 1978, Grenot 1976, Heatwole 1976, Huey 1974, Lee and Badham 1963, Licht and Basu 1961, Licht *et al.* 1966, McGinnis and Brown 1966, Norris 1953, Parker and Pianka 1974, Pentecost 1974, Pianka 1971, Pianka and Parker 1972, Pianka and Pianka 1976, Spellerberg 1972b, Vance 1973, Wilhoft 1958, Wilhoft and Anderson 1960.

Egg laying was delayed in the Gainesville pen. A female captured on April 4 laid in Gainesville on June 12, within the normal Caicos nesting season of the first two weeks in June. However, another female, which had been captive in Gainesville since July 30, 1974, laid in the pen on July 25, 1975. Yet another female, captive since February 25, 1976, laid on July 25. The rate of egg development may have been slower in Gainesville's cooler climate or shorter photoperiod (Mayhew 1961). However, the delays may also have been partially due to a lack of nesting burrows in the pen, resulting in egg retention. For example, a caged female on Water Cay, captured on June 5, did not lay until June 17.

Habitat Complexity

A foraging *Cyclura carinata*, a semiarboreal lizard sometimes traveling up to 1600 ft (488 m) a day, should receive a radiant heat input from direct and filtered sunlight that is inversely proportional to the density and height of the plants in its territory. If the habitat niche of the species is sufficiently broad, the regulating phase T_b of individual lizards should increase significantly as vegetational cover decreases. This has been demonstrated for the eurythermal lizard, *Anolis aculatus* (Ruibal and Philobosian 1970). *Cyclura* burrows were absent from both beach and swales, infrequent in Mixed Woodland, perhaps due to low food plant diversity, and infrequent in Mesic Coppice, perhaps due to insufficient open areas for basking. Iguanas once lived in all the other vegetation zones on Pine and Water Cays, reaching the highest density in Rocky Coppice. This generalist habitat niche is not surprising considering the lack of significant vertebrate competitors.

Monitoring sites were carefully chosen in order to find the maximum mean T_b difference due to differences in vegetational cover. The highest regulating phase T_b's were expected in the sparsely vegetated Open Scrub nearest the beach. However, man and his dogs had nearly extirpated the lizards from this zone by the time my study commenced. Therefore, Site I had to be located further inland in semi-Open Scrub bordering the Dense Scrub. Lizard T_b's were expected to be lowest at Site II, a thickly vegetated area covered with a mixture of Dense Scrub and Rocky Coppice, bordering a rocky coast. The site was crisscrossed by a network of bulldozed roads. On the average, bushes and trees were 63 percent taller at Site II than at Site I (Table 6). Site II also had approximately 82 percent more shade, when roads were excluded from the transects.

As expected, mean T_b was significantly higher at Site I, although the difference was not very great (mean difference = 1.6 C, Table 5). The small lizard sample sizes were compensated for somewhat by the long monitoring times. Inland environmental temperature and wind velocity differences between sites were negligible. Thus, the T_b difference was probably due to the vegetational cover difference. The site difference was significant in hyperthermic as well as nonhyperthermic lizards (Figure 12). The mean T_b difference was slightly less for maximally hyperthermic than for nonhyperthermic lizards. The high T_b distributions were negatively skewed while the low T_b distributions were more normally distributed.

Caged lizards were monitored in an attempt to produce a significant difference in mean T_b by varying the amount and kind of shade available in the lizard's habitat. It was hypothesized that, given only two burrows as heat sinks, each with relatively constant air and substrate

Figure 12. Influence of habitat on body temperature. Each upper frequency distribution is for three days of monitoring of a maximally hyperthermic adult male *Cyclura carinata* (Site I, solid line; Site II, dashed line). The lower distributions are for the same two lizards on the three days of lowest mean T_b, unaffected by long periods of overcast. Horizontal lines are ranges, vertical lines are mean T_b's, and rectangles are plus and minus two standard errors of the mean.

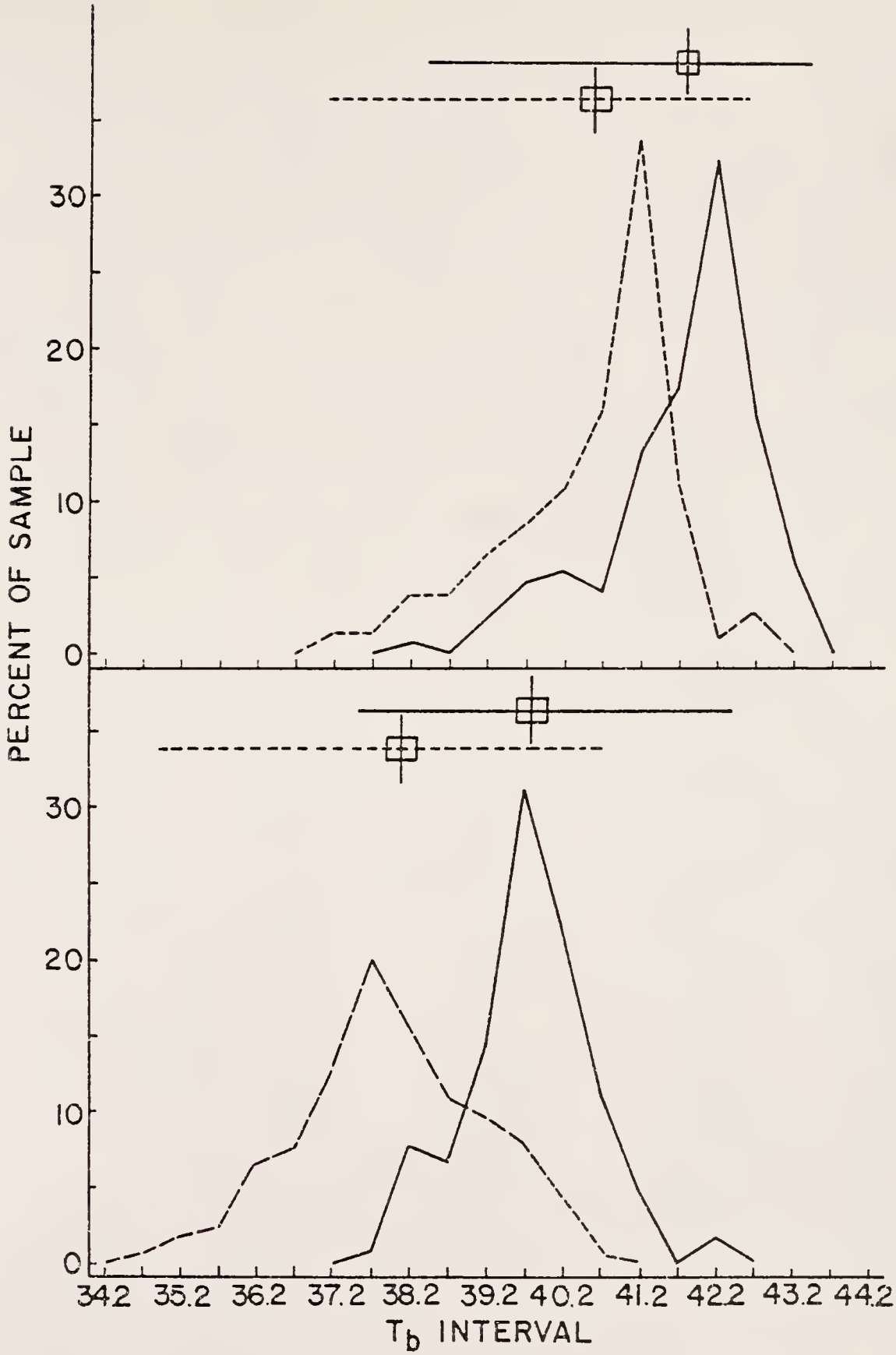

PERCENT OF SAMPLE
30
20
10
0
30
20
10
0
34.2
35.2
36.2
37.2
38.2
39.2
40.2
41.2
42.2
43.2
44.2
T_b INTERVAL

Table 6. Vegetational cover at Sites I and II on Water Cay. The height of a bush or tree was measured at approximately 7.5 m intervals along the transects, which were 30 m long.

	SITE I	SITE II
HEIGHT OF VEGETATION		
N (PLANTS)	20	20
MEAN HEIGHT (M)	1.77	2.88
2 SE	0.39	0.53
RANGE	0.79-3.88	1.12-4.57
PERCENT SHADE		
N (TRANSECTS)	5	5
MEAN PERCENT SHADE	43.3	79.0
2 SE	7.5	8.3
RANGE	33.1-51.7	68.9-90.4

temperatures below the lizard's minimum regulating phase T_b, mean T_b and the standard deviation of mean T_b would be greater than for the same lizard given vegetational shade, two burrows, and branches, which allowed greater convective cooling of lizards perched off the ground. Overall, mean T_b was significantly higher in the complex habitat ($p \leq 0.01$), but individually, this was true only for Lizard 5 (Table 7). The results may have been opposite to those expected because of lizard hyperthermia. Lizards 5-7 had their hyperthermic peaks while in the complex habitat, perhaps overriding the effect of the vegetational shade and the branches. The standard deviations of overall mean T_b in the two habitats were about the same, again contrary to expectation. The mean T_b of the four lizards caged in the complex habitat did not differ significantly from the two free-ranging lizards also monitored at Site I in June (Table 5). Clearly, caged *Cyclura* required only a very simple habitat to thermoregulate as well as free-ranging lizards.

Cloud Cover

Mean regulating phase T_b decreased linearly as overcast time increased (Figure 13). The correlation coefficient was significantly less than zero ($p \leq 0.0001$ for $r = -0.042$, $\bar{X}\ T_b = -0.042$ Percent Cloud Cover + 39.582). As expected, the correlation coefficient increased as the weather got colder (June-July, $r = -0.193$, N.S.; Oct, $r = -0.344$, N.S.; February, $r = -0.541$, $p \leq 0.01$). Mean T_b per day was never depressed below 36.5 C by cloud cover times of less than 30 percent of total time. Continuous overcast periods had to be fairly lengthy to depress mean T_b below the mean minimum T_b for clear weather, since

Table 7. Body temperature of *Cyclura carinata* confined to cages with two structurally different habitats. Lizards were first monitored in the complex habitat for three to four days, then in the simple habitat for two to five days.

	COMPLEX HABITAT					SIMPLE HABITAT				
LIZARD	DAYS	N	MEAN T_B	SD	2SE	DAYS	N	MEAN T_B	SD	2SE
4	3	60	39.9	1.17	0.30	2	48	40.4	1.40	0.40
5	4	101	41.1	0.85	0.17	3	95	39.6	0.87	0.18
6	3	64	38.1	1.10	0.28	5	97	37.7	1.54	0.31
7	4	104	38.8	3.54	0.69	3	90	38.2	1.15	0.24
Overall	14	329	39.7	1.63	0.18	13	330	38.8	1.60	0.18

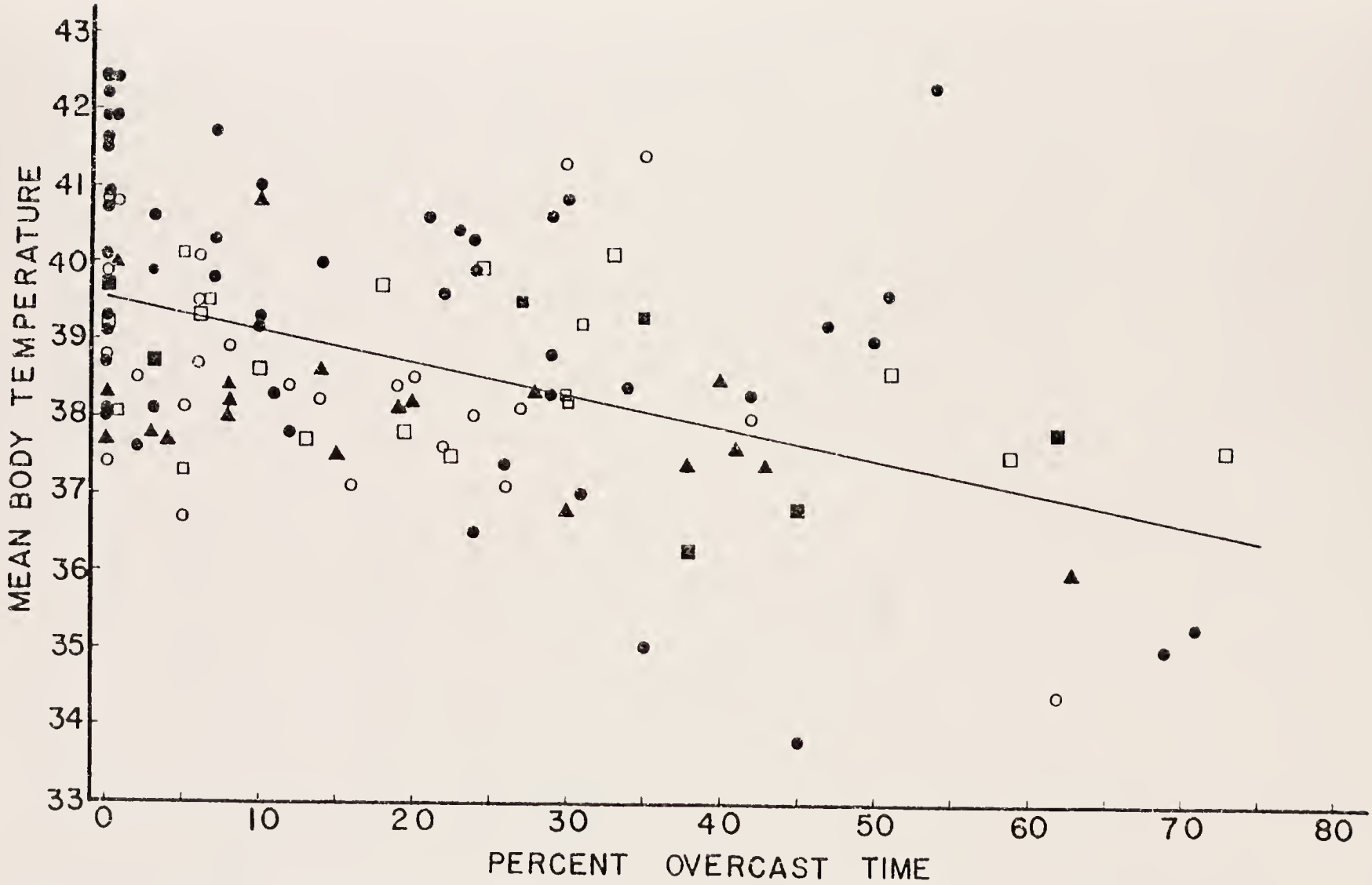
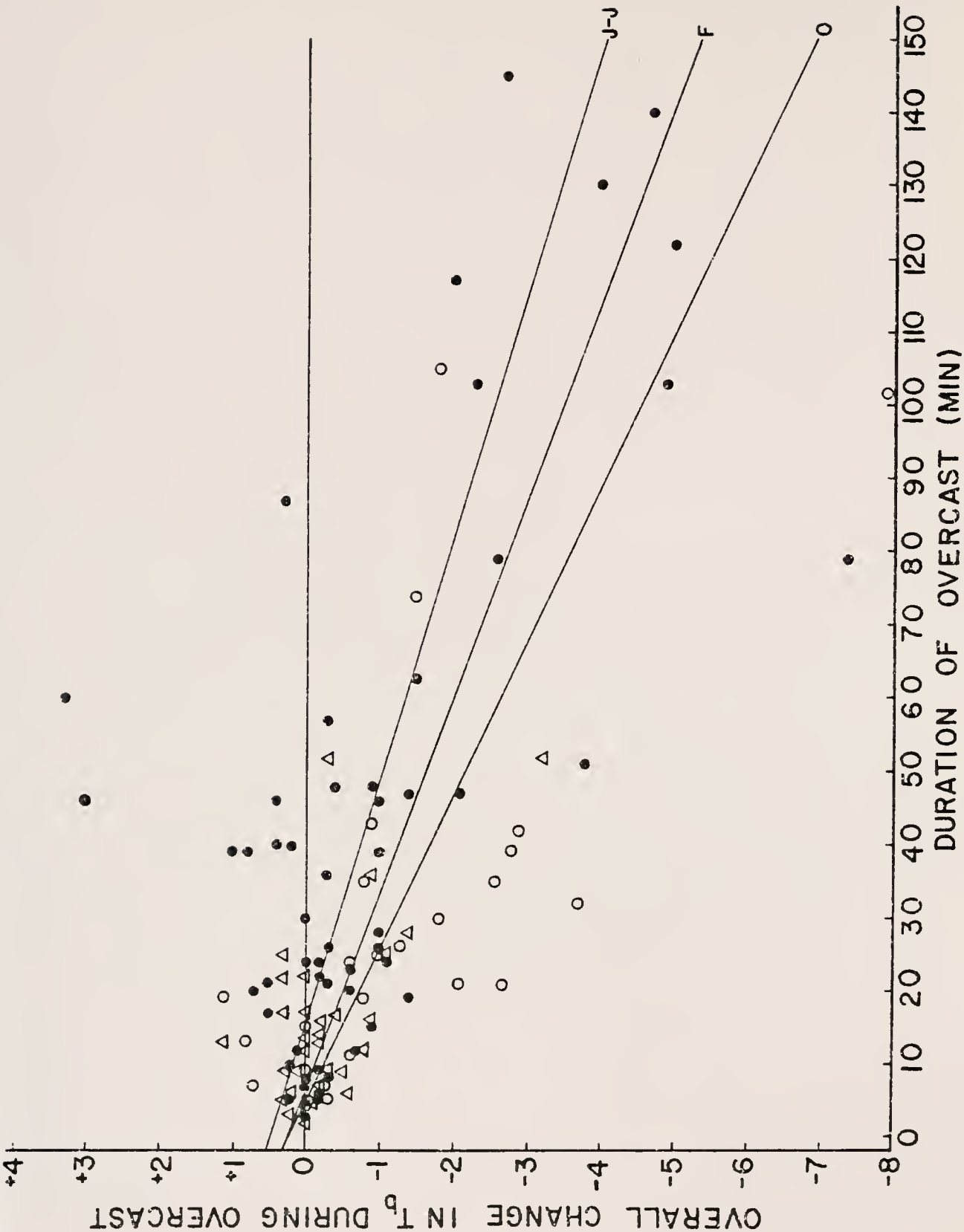


Figure 13. Effect of cloud cover on mean regulating phase body temperature. Practically all field monitoring is included (N = 124 days). Each symbol represents one day's monitoring; February (solid triangles), June (solid circles), July (open circles), August-September (solid squares), and October (open squares). The regression line was fitted by the method of least squares.

large adult *Cyclura* cooled slowly and radiative heat input continued during light overcast. The high mean T_b of 42.3 C during June, achieved with an overcast time of 54 percent, was possible due to the thinness of the cloud cover.

Lizard T_b sometimes increased rather than decreased during overcast periods, especially when the overcast lasted only a short time (Figure 14). When the lizard had been heating prior to the overcast, the post overcast T_b rise can be explained as a result of thermal lag. However, T_b also commonly rose initially during overcast after decreasing before overcast, the maximum T_b during overcast being higher than the previous maximum before overcast. Iguanas sought out hot substrates avoided while the sun was shining and assumed a prostrate posture (Figure 44, Illustrations 4 and 11). It appears that higher core T_b was tolerated under these conditions, since overheating, as indicated by body surface temperature, was not possible. The noises of lizard activity; that is, walking, chasing, arboreal feeding, and dropping to the ground after feeding, nearly ceased during extended overcast periods. Except for short walks, iguanas remained practically motionless until a few minutes after an extended overcast cleared. The abruptness of the activity cessation varied directly with the severity and duration of the overcast. Short periods of overcast, frequently encountered, resulted in little or no curtailment of activity. The T_b change during overcast differed slightly with season. On the average, T_b decreased 2.0 C per hour during February, 1.3 C during June-July, and 2.6 C during October, the month of heaviest overcast. A large increase in T_b was most likely during summer overcast.

Figure 14. Effect of overcast duration on lizard body temperature change. Data from February are indicated by open triangles, June and July by solid circles, and October by open circles. Regression lines were calculated by the method of least squares. All lizards were probably out of their burrows during the full overcast period.


OVERALL CHANGE IN T_b DURING OVERCAST
+4
+3
+2
+1
0
-1
-2
-3
-4
-5
-6
-7
-8
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
DURATION OF OVERCAST (MIN)
J-J
F
O

Shaded Air Temperature

In Huey and Slatkin's cost-benefit model for thermoregulation (1976), the value k represents a lizard's "thermoregulatory strategy," varying from perfect thermoregulation (k = 0) to passive nonregulation (k = 1). The linear regression coefficient r for a graph of T_b vs. shaded T_a at the lizard's body surface is a good estimate of k. A lizard living in a tropical forest would be expected to have a high r value, since direct solar radiation near the forest floor is only patchily available. On the other hand, regulating phase T_b should be practically independent of shaded T_a in a heliothermic lizard like *Cyclura*, living in fairly open habitats. *Cyclura*, with its low r values, is a nearly perfect thermoregulator (Figure 15; r = 0.151 in Graph 1, 0.013 in Graph 2, 0.131 in Graph 3, and 0.154 in Graph 4).

Mean T_b-T_a during the regulating phase at Site II was least in July ($\bar{X}$ = 5.9 C, SD = 2.00, Range = 1.2-10.4 C, N = 68), greater in October ($\bar{X}$ = 7.2 C, SD = 1.65, Range = 4.2-12.2 C, N = 67), and greatest in February ($\bar{X}$ = 11.0 C, SD = 2.11, Range = 5.5-15.6 C, N = 58), since shaded air temperature decreased faster seasonally than T_b, again expected in a heliotherm.

One problem with this analysis is that the air temperature was not measured at the surface of the lizard, but rather at a site near the blind. An attempt was made to select the lowest shaded air temperature at the site. The assumption was made that this air temperature was also available to the lizard. If this assumption is correct, the value of r is still a measure of the degree of heliothermy. Of course, the correlation of any instantaneous thermal input with core T_b declines as body size increases in a lizard moving rapidly through a varied thermal environment.

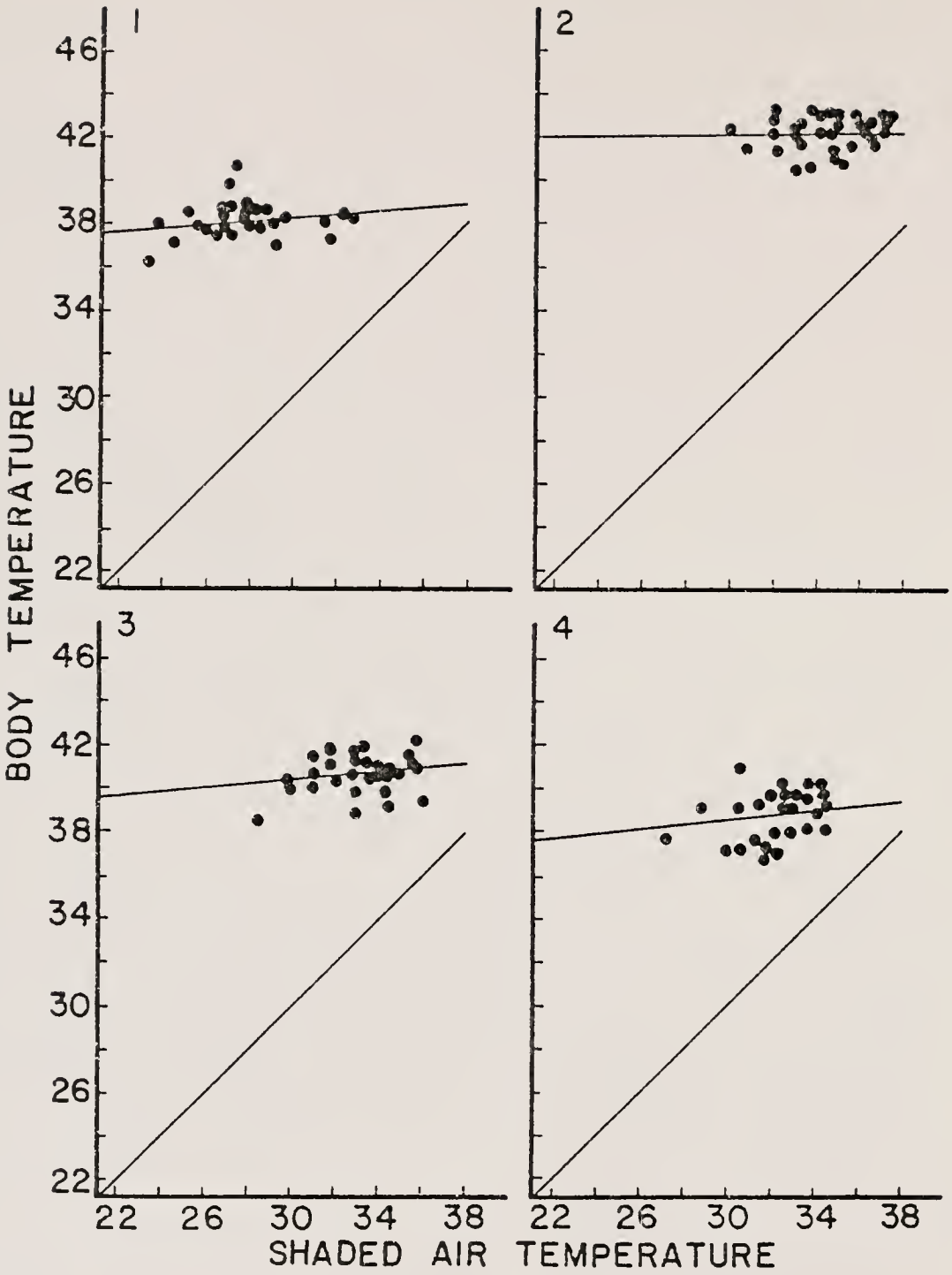
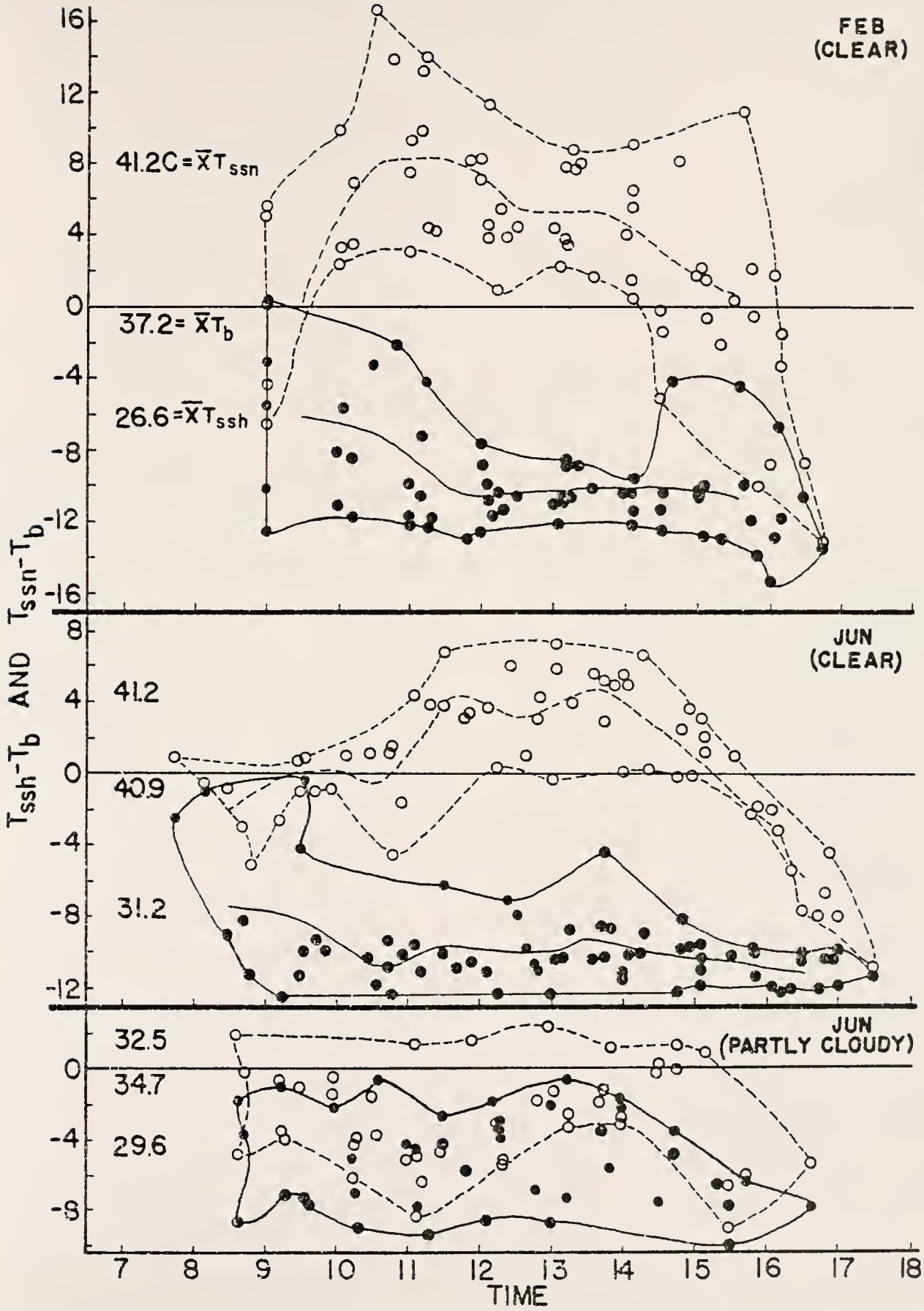


Figure 15. Correlation of lizard body temperature during the regulating phase with shaded air temperature. Each graph represents the data for one dominant male (Graph 1, Lizard 3; Graph 2, Lizard 9; Graph 3, Lizard 11; Graph 4, Lizard 3). T_b was independent of shaded air temperature in all four lizards. Data were collected on five to seven clear days in February (Site II), June (Site I), July (Site II), and October (Site II), respectively.

Substrate Temperature

Heliothermic lizards are able to behaviorally maintain body temperature within narrow limits, somewhat independently of ground surface temperatures, which fluctuated with changes in daily and seasonal thermal flux, cloud cover, and wind speed. McGinnis (1970) coined the term "thermoregulatory flexibility" for this ability of heliothermic lizards. Even during the hottest days, shaded substrates other than in burrows were available at temperatures well below lizard T_b (Figure 16). Iguanas rested quietly in the shade during maximum midday insolation rather than retreating to a burrow, in a posture somewhere between prostrate and upright (see Figure 44). T_b was usually considerably less than the sand surface temperature in the sun (T_{ssn}) on clear days, except during the early morning and late afternoon (upper and middle graphs). Hyperthermic lizards in June decreased the T_{ssn}-T_b difference more than February nonhyperthermic lizards by spending considerable time in exposed areas. Iguanas remained above ground during mildly heavy overcast on partly cloudy days, receiving maximum insolative heat input with minimum convective heat loss by sitting in exposed areas protected from the wind. T_b was commonly higher than T_{ssn} under these conditions (lower graph). Nonetheless, T_b eventually decreased during extended overcast. T_b decreased more slowly than T_{ssn} in the late afternoon on clear days due to the longer heat retention time of the lizard's body than the surface of the windswept sand. The negative T_{ssn} -T_b difference in the late afternoon was not as great as shown in the middle graph, however. Large males, the last lizards to submerge, sought out the last remaining sunspots in the habitat, unavailable to me for temperature measurements without disturbing the lizards. Also,

Figure 16. Thermoregulatory flexibility. T_b's of emergent lizards have been subtracted from the sand surface temperature in the shade (solid circles, $T_{ssh} - T_b$) and from the surface temperature of sand continually exposed to the sun (open circles, $T_{ssn} - T_b$). Solid and dashed lines encompass the $T_{ssh} - T_b$ and $T_{ssn} - T_b$ values, respectively. Solid and dashed lines also indicate the hourly mean values (upper two graphs only). Data for the upper, middle, and lower graphs were collected on 14 clear days in February at Site II, 8 clear days in June at Site I (lizards hyperthermic), and 5 partly cloudy days in June at Site I, respectively. Mean T_{ssh}, T_b, and T_{ssn} values are given on the left side of each graph.


FEB
(CLEAR)
41.2C=$\bar{X}T_{ssn}$
37.2=$\bar{X}T_b$
26.6=$\bar{X}T_{ssh}$
JUN
(CLEAR)
41.2
40.9
31.2
JUN
(PARTLY CLOUDY)
32.5
34.7
29.6
$T_{ssh}-T_b$ AND $T_{ssn}-T_b$
TIME
16
12
8
4
0
-4
-8
-12
-16
7
8
9
10
11
12
13
14
15
16
17
18

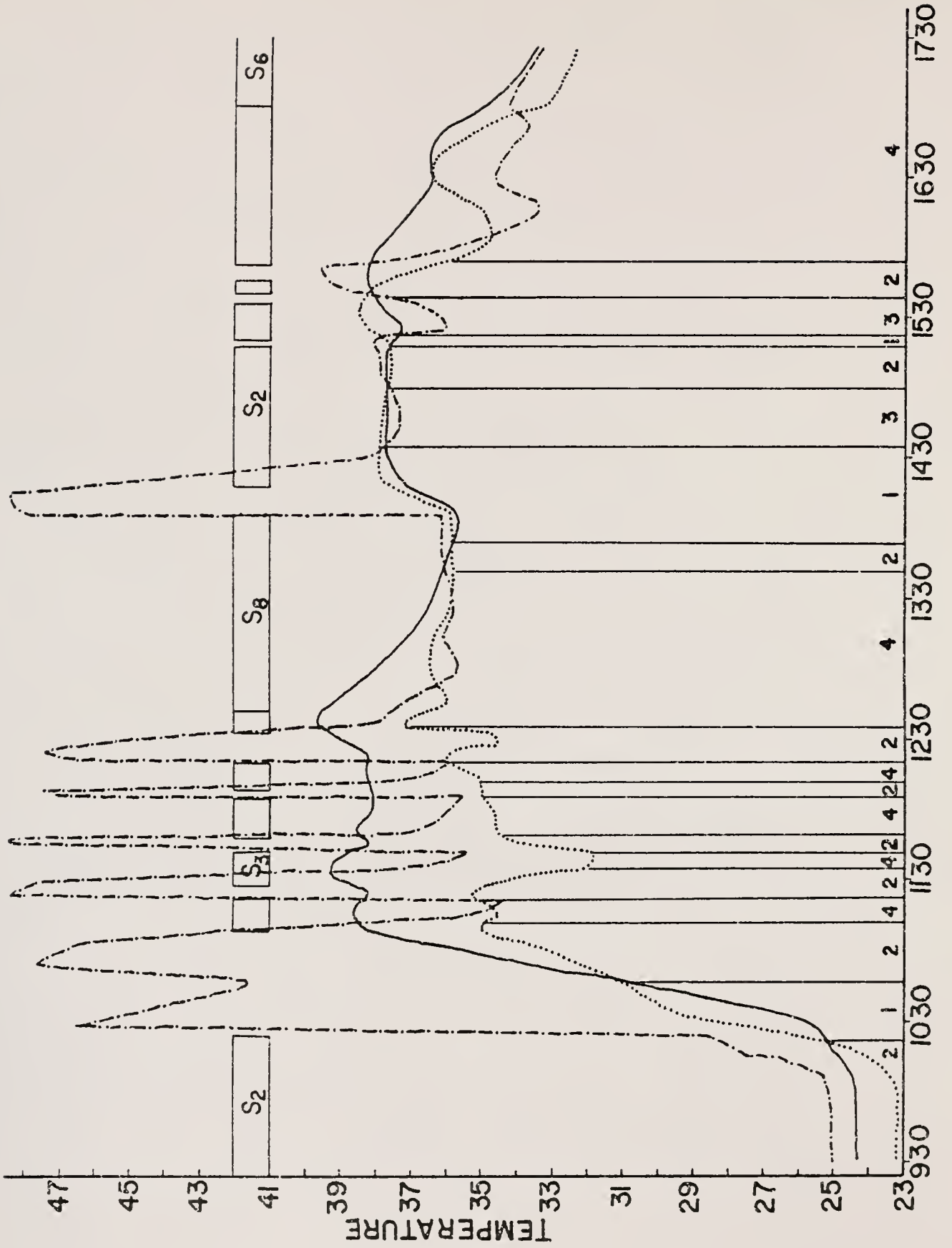
iguanas kept their ventral body surfaces in contact with the substrate during this period. The sand surface temperature important in conductive heat exchange, lying beneath the motionless lizard's body, did not decrease as rapidly as T_{ssn}.

Patterns of Heat Transfer between Penned Iguanas and their Environment: The Three-Transmitter Study

Heat transfer occurs everywhere on the lizard's body surface. Dorsal heat exchanges are primarily radiative and convective while ventral exchanges are also conductive. Heat loss due to evaporation of water from cutaneous and respiratory surfaces and heat gain due to metabolism and condensation of water vapor will be assumed to be approximately equal in the following analyses and thus, ignored. Based on temperature received from the dorsal surface, gut, and ventral surface transmitters, four heat transfer conditions were possible: 1. The lizard simultaneously received a net heat input from both dorsal and ventral body surfaces, that is, both the dorsal and ventral transmitter temperatures were higher than the gut temperature, 2. the lizard received heat dorsally and lost it ventrally, 3. lost heat dorsally and gained it ventrally, and 4. lost heat both dorsally and ventrally. All four heat transfer conditions usually occurred sometime during an emergent lizard's day, as illustrated in Figure 17 for a large male.

Three problems concerning the limitations of the transmitter technique should be pointed out. Ideally, the time constant for transmitter sensing of a rapid temperature change in the environment should be infinitely small. However, this was not the case. For example, the lizard in Figure 17 moved to the shade at 1109, resulting

Figure 17. Three transmitter records of a large male *Cyclura carinata* in the Gainesville pen on August 21, 1975. The lizard's black body temperature at five mm above and immediately anterior to the rear legs, gut temperature, and ventral surface temperature, also just anterior to the rear legs, are represented by the dot and dash line, solid line, and dotted line, respectively. The lizard was in the shade much of the day (rectangles), occasionally entering different plywood shelters (S_2, S_3, etc.). Transitions from one heat transfer condition to another are demarcated by vertical lines and labeled by number at the bottom of the graph. The heat transfer conditions are: 1) dorsal and ventral surface temperatures higher than the gut (core) temperature, 2) dorsal surface higher, ventral surface lower than the core, 3) dorsal surface lower, ventral higher than the core, and 4) both surfaces lower than the core. The day was almost perfectly clear.


TEMPERATURE
47
45
43
41
39
37
35
33
31
29
27
25
23
930
1030
1130
1230
1330
1430
1530
1630
1730
S2
S8
S3
S6

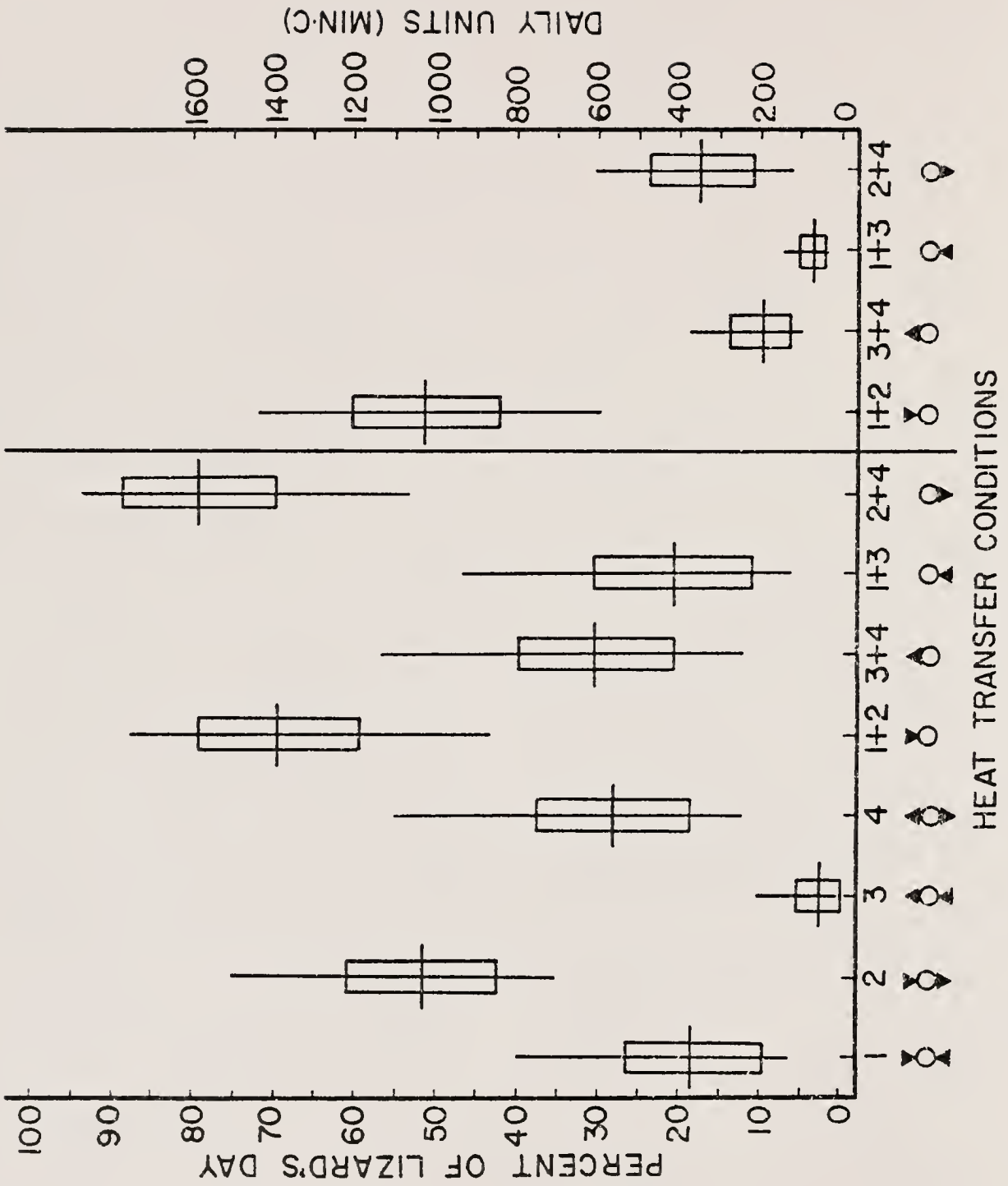
in a rapid change from Condition 2 to Condition 4. When the transition time was taken from the temperature records, however, Condition 4 did not start until 1112. The second problem was the small number of transmitter monitoring sites. Large heat exchange differences often occurred at different locations on the lizard's body surface. For example, the anterior portion of the lizard was often in the shade while the dorsal black body probe was in the sun. Also, fairly large internal temperature differences occurred, as between the head and the gut. It is undoubtedly technically feasible to double or triple the number of temperature monitoring sites on a free-ranging lizard the size of an adult male *Cyclura*. Thirdly, the surface probes should have been implanted subcutaneously, since temperatures there were probably of greater biological significance. The temperature difference was probably minimal between the subcutaneous area and the ventral surface as measured. However, dorsal black body temperature probably differed somewhat from the dorsal skin surface temperature. Hopefully, since the thermal lag time of the transmitter probe was less than the subcutaneous area, the calculated times for the heat transfer conditions were not grossly inaccurate.

Several patterns of heat transfer were consistently observed during the morning heating and regulating phase. Only Conditions 1 and 2 occurred during the morning heating phase on clear days. Typically, lizards emerged from the plywood shelters and, after a short delay, walked to a sunlit patch in the still partially shaded pen, where sand surface temperature exceeded gut temperature. The resulting Condition 1 lasted a variable portion of the morning heating phase, depending on whether, how soon, and how many times the animal moved to another sunlit

area. Condition 4 typically alternated with Condition 2 during the early regulating phase, when lizards shuttled at a high rate. As substrate temperatures rose and lizards tolerated these higher temperatures, Conditions 3 and 1 became more common. Lizards probably tolerated higher body surface temperatures than core temperatures, as evidenced by the mean maximum temperature of the dorsal black body transmitter ($\bar{X}$ = 45.8 C, SD = 2.0, Range = 40.6-50.0) exceeding the mean maximum of the gut ($\bar{X}$ = 38.3 C, SD = 1.0, Range = 36.1-39.7). However, the mean maximum black body temperature did not exceed the critical thermal maximum of the core ($\bar{X}$ = 46.2 C). Lizards commonly returned to the plywood shelters for lengthy periods during midday hours, where nearly stable body temperatures were eventually temporarily attained (Figure 17). Lizards usually avoided the shaded sand available underneath the shelters during this time in favor of the higher temperatures in the shelters. The same shade choice selectivity with resultant T_b stabilization was observed in the field. Condition 4 predominated when the pen became shaded in the afternoon, since lizard surface temperatures declined faster than gut temperature. By seeking out relatively warm, recently shaded substrates and assuming a prostrate posture, lizards temporarily stopped their core temperature decline (Figure 17, 1630-1642). They were not usually thigmothermic during this time, however, since ventral surface temperature did not usually rise above core temperature.

The most common heat transfer condition was Number 2, occurring an average of 51.3 percent of the morning heating plus regulating phases (Figure 18, left graph). Condition 3 occurred only 2.5 percent of the

Figure 18. Partitioning of heat transfer in active penned *Cyclura carinata*. Three large males were monitored sequentially in August for a total of eight days. The times the lizard spent in each of the four heat transfer conditions during morning heating and regulating phases are graphed on the left. In the right graph, dorsal and ventral heat gains are compared relative to dorsal and ventral heat losses, respectively. Circles symbolize lizard core temperature. An arrow points toward or away from a circle when dorsal or ventral surface temperature is greater or less than core temperature, respectively. Horizontal lines are means, vertical lines are ranges, and rectangles are plus and minus two standard errors of the mean.


PERCENT OF LIZARD'S DAY
0
10
20
30
40
50
60
70
80
90
100
DAILY UNITS (MIN·C)
0
200
400
600
800
1000
1200
1400
1600
1
2
3
4
1+2
3+4
1+3
2+4
HEAT TRANSFER CONDITIONS

time, restricted to the regulating phase. Lizards gained heat dorsally more of the time than they lost heat and were thigmothermic only 20.7 percent of the day, 9.3 percent during the short morning heating phase. To crudely compare dorsal heat gain with loss and ventral heat gain with loss, the area between gut and dorsal black body temperature lines and gut and ventral surface temperature lines in graphs like Figure 17 were measured with a planimeter. *Cyclura* gained approximately five times more heat than it lost dorsally and lost five times more heat ventrally than it gained (Figure 18, right side). This is a quantitative way of saying the lizard was a heliotherm rather than a thigmotherm.

Average core body temperature increased most rapidly during Condition 1, followed by Conditions 2, 3, and 4, respectively (Figure 19). Morning heating rates were significantly higher than heating rates of the same Conditions 1 and 2 during the regulating phase. The maximum rate recorded, +20.5 C/hr, occurred during Condition 1 during morning heating. The variance of mean T_b change was highest for Condition 2 during both the morning heating and regulating phases, due to the wide range of radiative and convective heat inputs vs. conductive heat losses possible during this condition. Iguanas occasionally cooled during Condition 2 when substrate heat loss exceeded dorsal gain.

The number of daily heat transfer conditions was linearly and directly related to daily lizard activity (Figure 20, left graph). The correlation was nearly perfect. The line extrapolated to practically zero heat transfer conditions at zero activity. The relationship is intuitively obvious; the more the lizard moves in the pen, the greater the number and variety of thermal environments it encounters. The number of heat transfer conditions was also linearly and directly related

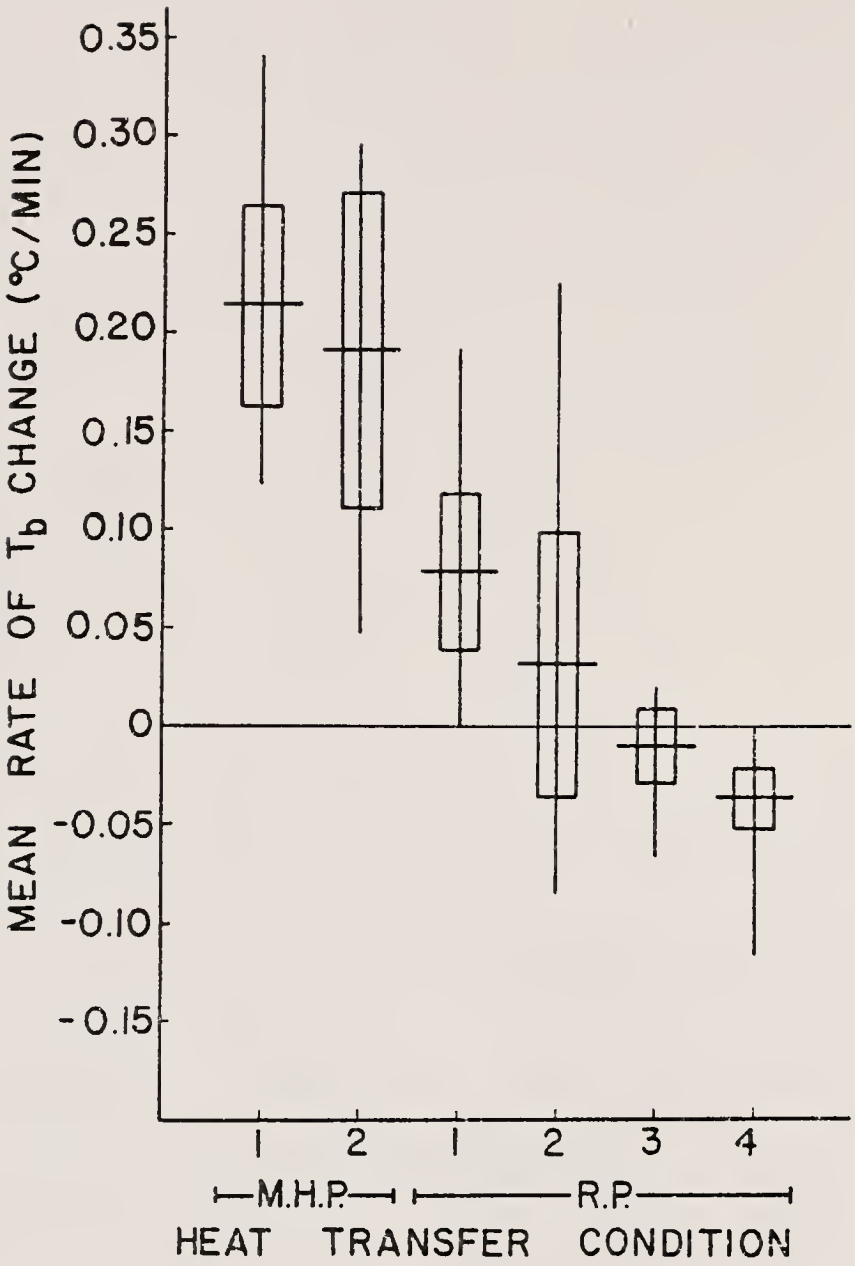
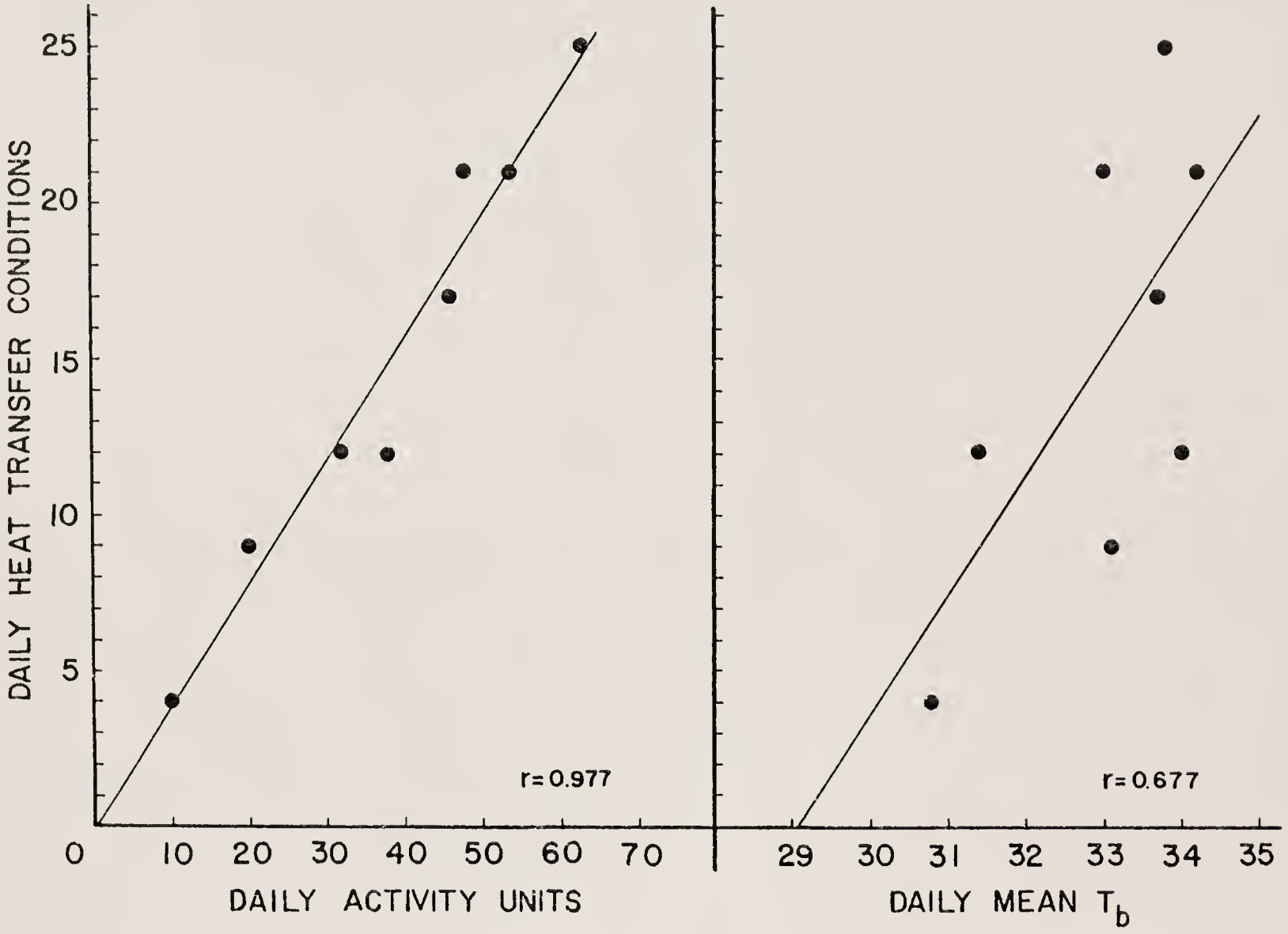


Figure 19. Rate of core body temperature change during the four heat transfer conditions. Rates during both the morning heating and regulating phases (M.H.P. and R.P.) are given. Three male lizards were used, weighing 1195, 1240, and 1260 g. Horizontal lines are means, vertical lines are ranges, and rectangles are plus and minus two standard errors of the mean.

Figure 20. Correlations of the sum of daily heat transfer conditions with lizard activity and mean body temperature. An activity unit is any behavioral sequence; a walk between two points, a feeding bout, digging sand at the pen wall, etc. The mean T_b's were calculated for the morning heating plus regulating phases. Correlation coefficients for the regression lines are given at the bottom of each graph. Data were collected for three males in the Gainesville pen over a period of eight days.


DAILY HEAT TRANSFER CONDITIONS
25
20
15
10
5
0
10
20
30
40
50
60
70
DAILY ACTIVITY UNITS
r=0.977
29
30
31
32
33
34
35
DAILY MEAN T_b
r=0.677

to mean T_b (Figure 20, right graph), but the r value was not as great ($p \leq 0.05$). The regression line extrapolated to 29.1 C mean T_b at zero heat transfer conditions, approximately equal to the mean T_b of summer lizards in the field just prior to emergence. This relationship is intuitively obvious; as overcast skies decrease per day, lizard mean T_b and activity and the number of thermal environments available to the lizard all increase.

Statistical Analyses of Regulating Phase Body Temperature

Body Temperature Maxima and Minima

Heath (1970) proposed that the thermoregulatory behavior of lizards is controlled by maximum and minimum limit temperatures or setpoints separated by a nonthermoregulatory zone. Lizards seek shade when the maximum limit temperature is reached, a mandatory behavior since further rise in T_b results first in panting, then paralysis and death. Sun seeking behavior occurs at the minimum limit temperature and is also mandatory, since temperature dependent processes such as recovery from lactic acid debt following activity proceed at such slow rates below the minimum T_b that lizard efficiency is considerably reduced. Due to the daily cyclic change in available environmental temperatures, maximum and minimum limit temperatures may be of little importance to the lizard early and late in the day and during the middle hours, respectively.

Maximum and minimum limit temperatures can be accurately determined only in two-temperature selection experiments, with lizards shuttling between two chambers at constant ambient temperatures known to lie above

and below the limits (Berk and Heath 1975a, b, Barber 1976). Non-thermoregulatory movements have no effect on T_b maxima and minima in two-chamber experiments. However, in continuous gradient experiments and in the field, the same movements can add intermediate minimum and maximum T_b's, which inaccurately narrow the temperature range between mean value estimates of the limit temperatures. Also, maximum and minimum T_b's often occur in motionless lizards in the field; that is, at the start and end of overcast periods and when radiant input wanes late in the day. However, these nonthermoregulatory values were easily identified on the T_b records and omitted from analysis.

Frequency distributions of minimum regulating phase T_b's were commonly negatively skewed, whereas maximum T_b's were commonly positively skewed (Table 8). The statistic a_3 (Remington and Schork 1970) was used to estimate the degree of skewness and test for it in samples larger than 25. Values were commonly negative (10 of 15) for minimum T_b's and positive (12 of 15) for maximum T_b's. However, the results showed disconcerting inconsistencies, even when sample sizes were adequately large for significance testing. All minimum and maximum T_b frequency distributions were normal for *Dipsosaurus dorsalis* monitored in a two-chambered gradient (Barber and Crawford 1977), in contrast to the *Cyclura* results in a continuous gradient and in the field.

The standard deviation of the mean of the T_b maxima (SD_{max}) was not significantly different from the SD of the mean of the minima (SD_{min}, F-test, $p \leq 0.05$) in any lizard monitored in the field or continuous thermal gradient (Table 9). In contrast, Berk and Heath (1975a) found the average SD of the minima to be significantly greater than the maxima

Table 8. Skewness of frequency distributions of minimum and maximum body temperatures. Each lizard's mean daily T_b varied less than 1 C for the days in the sample. Field minimum and maximum T_b's occurred during times of unobscured sun. Only Lizard 9 was hyperthermic.

			MINIMUM T_B'S			MAXIMUM T_B'S		
MONTH	LIZARD	LOCATION	N	Skewness (a_3)	P	N	Skewness (a_3)	P
Feb	2	Free-Ranging	18	-0.941	--	19	+0.019	--
Feb	3	Free-Ranging	35	+0.356	NS	48	+0.754	0.05
June	7	Caged	28	+0.221	NS	34	+0.084	NS
June	8	Free-Ranging	22	-0.864	0.05	28	+1.874	0.01
June	9	Free-Ranging	24	-0.439	0.05	30	-0.393	NS
July	10	Free-Ranging	26	-0.884	0.05	33	-0.003	NS
July	11	Free-Ranging	35	-0.250	NS	43	+0.069	NS
Oct	2	Free-Ranging	12	-0.552	--	17	+0.177	--
Oct	3	Free-Ranging	38	+0.072	NS	57	+0.606	0.05
Field Lizards ($\bar{X}$)				-0.365			+0.354	
Dec	1	Gradient	13	-0.386	--	17	+0.066	--
Jan	3	Gradient	26	-0.808	0.05	31	+0.236	NS
Jan	4	Gradient	43	+0.645	0.05	55	+0.972	0.01
July	3	Gradient	14	-0.596	--	16	+0.922	--
July	5	Gradient	17	-0.498	--	22	-1.173	--
Aug	6	Gradient	17	+1.070	--	18	+1.154	--
Gradient Lizards ($\bar{X}$)				-0.096			+0.363	

Table 9. Means and standard deviations of minimum and maximum body temperatures of individual lizards and correlation of maximum vs. minimum and minimum vs. maximum T_b pairs. An asterisk indicates the correlation was significant ($p \leq 0.01$).

MONTH	LIZARD	LOCATION	T_B MINIMA $\bar{X}$	T_B MINIMA SD	T_B MAXIMA $\bar{X}$	T_B MAXIMA SD	SD MINIMA÷ SD MAXIMA	MAX-MIN CORRELATION PAIR (r)	MIN-MAX CORRELATION PAIR (r)	NUMBER OF SHUTTLE PAIRS (N)
Feb	2	Free-Ranging	37.6	1.06	38.5	0.97	1.09	0.802*	0.549*	34
Feb	3	Free-Ranging	38.0	1.06	38.8	1.09	0.97	0.876*	0.842	51
June	4	Caged	38.7	1.18	41.1	1.26	0.94	0.338	0.383	24
June	5	Caged	39.6	1.37	40.8	1.17	1.17	0.833*	0.811	36
June	6	Caged	37.2	1.16	38.5	1.04	1.12	0.714*	0.614*	27
June	7	Caged	37.8	1.53	39.4	1.25	1.22	0.792*	0.849*	39
June	8	Free-Ranging	38.7	2.58	40.3	2.07	1.25	0.925*	0.857*	40
June	9	Free-Ranging	40.8	1.44	41.5	1.30	1.11	0.937*	0.921	46
July	10	Free-Ranging	38.0	1.84	39.3	1.68	1.10	0.896*	0.861*	56
July	11	Free-Ranging	39.0	1.68	40.1	1.49	1.13	0.864*	0.827*	52
Oct	2	Free-Ranging	38.7	0.93	39.6	0.81	1.15	0.584*	0.462	16
Oct	3	Free-Ranging	37.8	1.59	39.0	1.41	1.13	0.800*	0.740*	43
Field Lizards ($\bar{X}$)			38.5	1.45	39.7	1.30	1.12	0.780	0.726	
July	3	Gradient	35.6	1.47	37.8	2.01	0.73	0.664*	0.057	15
July	5	Gradient	36.5	2.37	38.3	2.00	1.18	0.554*	0.546*	18
Aug	6	Gradient	35.4	1.56	37.4	1.58	0.99	0.708*	0.849*	20
Aug	7	Gradient	36.2	2.35	39.9	1.54	1.52	0.261	0.287	10
Dec	1	Gradient	36.3	0.86	37.6	0.74	1.17	0.167	0.647	13
Jan	4	Gradient	36.8	0.74	37.7	0.80	0.92	0.651*	0.587	45
Jan	3	Gradient	37.7	0.83	38.8	0.61	1.36	0.660	0.548	28
Gradient Lizards ($\bar{X}$)			36.4	1.45	38.2	1.33	1.09	0.524	0.503	

for *Dipsosaurus dorsalis* confined to a two-chamber thermal gradient (1.91 ± 0.40 SD for the minima, 1.27 ± 0.29 SD for the maxima in *Dipsosaurus*, 1.45 ± 0.69 and 1.33 ± 0.60 SD for *Cyclura*). SD_{max} was tightly coupled to SD_{min} in individual lizards in the field: SD_{max} = 0.728 SD_{min} + 0.238 (r = 0.970, $p \leq 0.0005$, N = 12). The linear regression equation for the thermal gradient data was practically identical: SD_{max} = 0.694 SD_{min} + 0.316 (r = 0.804, $p \leq 0.025$, N = 7). However, the correlation was not as good. SD_{min} increased faster than SD_{max}. The linear regression equation for Berk and Heath's data for *Dipsosaurus* was SD_{max} = 0.316 SD_{min} + 0.673 (r = 0.435, $p \leq 0.005$, N = 36). The correlation coefficient was considerably smaller than for the *Cyclura* data, yet the correlation was still significant. Again, SD_{min} increased faster than SD_{max}. This is logical, since maximum T_b's are closer to the critical thermal maximum than minimum T_b's. SD_{min} and SD_{max} were uncorrelated with their mean T_b's (SD_{min} = 0.060 $\bar{X}\ T_{b\ min}$ - 0.841, r = 0.131, $p > 0.05$, N = 12, SD_{max} = 0.095 $\bar{X} T_{b\ max}$ - 2.464, r = 0.283, $p > 0.05$, N = 12). That is, lizards regulating at higher overall mean T_b's did not have significantly higher or lower spread to their minimum and maximum T_b's than lizards regulating at lower overall mean T_b's.

Frequency distributions of *Cyclura* minimum and maximum T_b's overlapped considerably. When a frequency distribution was compiled for the difference between the lowest daily maximum and the highest daily minimum T_b for 70 days of summer monitoring, the distribution was normal, with a mean of 0.8 C overlap (SD = 1.2 C) and only 15 days (22 percent of the total days) without any overlap. Berk and Heath found no overlap in their *Dipsosaurus* maxima vs. minima (maxima $\bar{X}$ ± SD = 41.7 ± 1.66 C, minima = 36.4 ± 1.12 C). Again, the difference in overlap may be

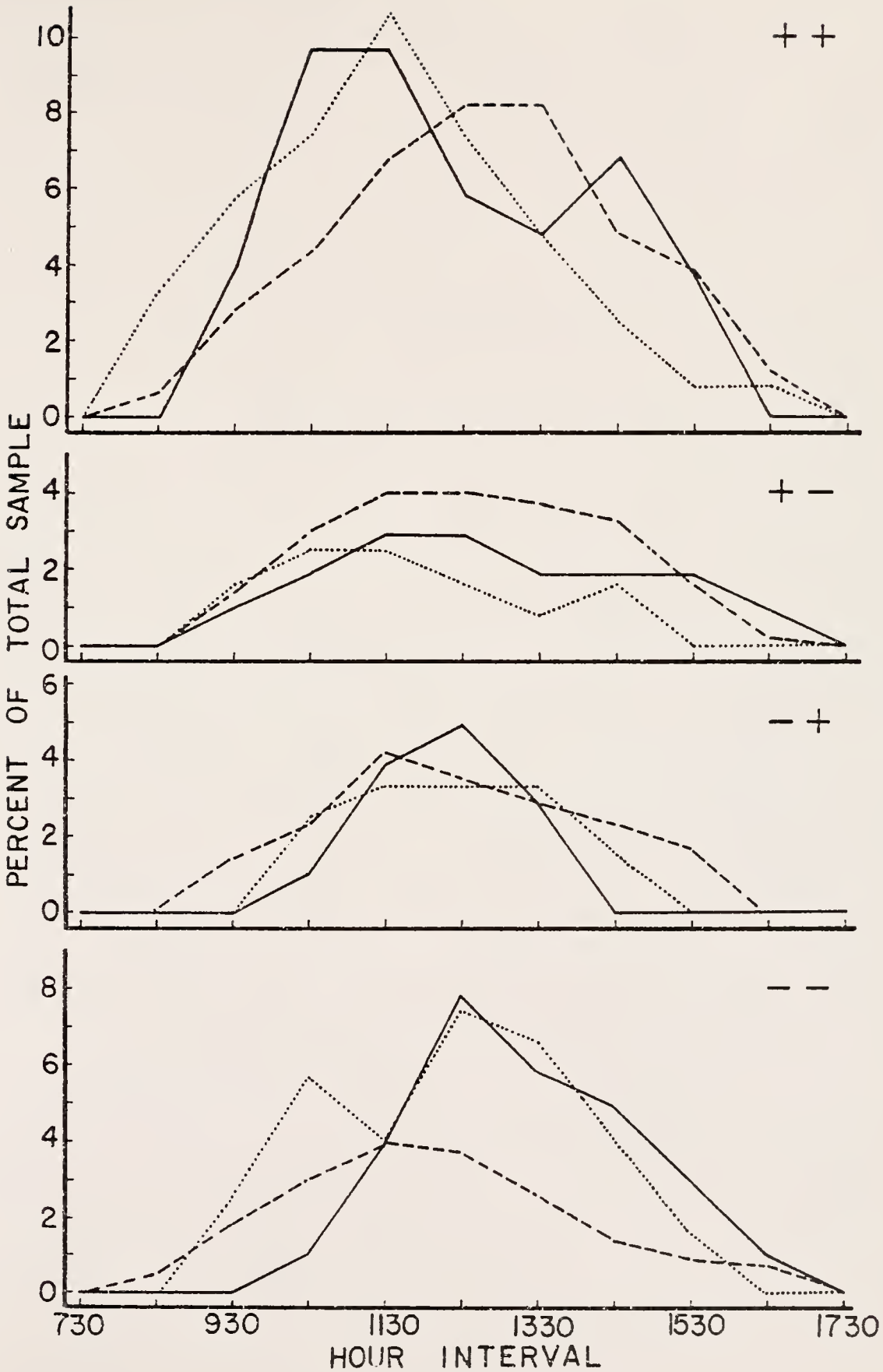
primarily due to comparing field and continuous gradient data for *Cyclura* with two-chamber gradient data for *Dipsosaurus*.

A Berk and Heath analysis (1975a) was used to determine how well minimum and maximum T_b's were correlated with each other (Table 9). The first daily maximum T_b and subsequent minimum formed one correlation pair and the same minimum and the second daily maximum formed another. The pairings were continued until all the regulating phase maxima and minima for the day had been included, excluding those during overcast periods. The correlation coefficient for linear regression, r, was used as the test statistic. Four correlation combinations were possible: one or both max-min and min-max pairs uncorrelated (0,+; 0,-; 0,0), both pairs positively correlated (+,+), both pairs negatively correlated (-,-), and one pair positively, one negatively correlated (+,-). All the r values were positive in both field and gradient samples and the majority of the correlations (68 percent) were significantly (+,+). On the average, correlations were higher in the field than in the gradient. In contrast, examples of all correlation combinations except (+,-) were found by Berk and Heath in their *Dipsosaurus* sample: 78 percent (0,+; 0,-; 0,0), 8 percent (-,-), and only 14 percent (+,+). The r value averages for the max-min and min-max correlation pair samples were both practically zero (0.070 and 0.022, respectively; N = 36 lizards).

The most important reason for the difference between *Cyclura* and *Dipsosaurus* in the Berk and Heath analysis would seem to be the differences in environmental temperature regimes the two species were subjected to. Maximum and minimum T_b's in *Cyclura* were not totally independent of the cyclic daily rise and fall in environmental temperatures. The lower r values for gradient than field correlations in Table 9 are in agreement

with this. The following data analysis was used to look more closely at the problem. In a continuous sequence of two maximum and two minimum T_b's, all different, there are four possible combinations; both the second maximum and the second minimum are greater than the first maximum and minimum (+,+), the second maximum is larger than the first while the second minimum is less than the first minimum (+,-), the second maximum declines while the second minimum increases (-,+) and both second maximum and minimum decline (-,-). Each hour over which the sequence extends can be assigned a unit quantity of one. Then, a frequency distribution for each combination can be computed for each month's sample of field data, as is illustrated in Figure 21. The +,+ combination was the most common (44.6, 41.8, and 43.5 percent of total hourly units for February, June-July, and October, respectively). This is expected due to the low rate of cooling in a large, frequently moving animal encountering higher temperatures as midday approached. As expected, the +,+ peak came latest in the day in the hottest months of June and July and earliest in the coolest month of February. The -,- combination peak fell at the noon hour in the cooler months of February and October, when the lizard was more likely to sit in a cool spot capable of reducing the second maximum or minimum T_b. The percent of total hourly units for -,- was lowest in the hottest months (18.9 percent in June-July vs. 27.3 and 32.0 percent for February and October, respectively). When the +,+ and -,- categories were summed and compared with the summed +,- and -,+ categories, the former were greater than the latter for all three months (February, 71.9 vs. 28.1 percent; June-July, 60.6 vs. 39.4; October, 75.4 vs. 24.6). The results for the thermal gradient were practically equal (53.2 vs. 46.8 percent), again

Figure 21. Time distributions of four combinations of maximum and minimum body temperature. In a sequence of two maximum and two minimum T_b's in a lizard's daily record, the second maximum can be greater than the first maximum and the second minimum can be greater than the first minimum (+,+), the second maximum greater and the second minimum less (+,-), the second maximum less and the second minimum greater (-,+), or both second maximum and minimum less (-,-). When each hour of each sequence (sequences overlap by one maximum and one minimum) is assigned a unit quantity of one, a frequency distribution of the timing of each combination can be tabulated. Solid, dashed, and dotted lines designate the February, June-July, and October field samples, respectively.


+ +
+ −
− +
− −
PERCENT OF TOTAL SAMPLE
0
2
4
6
8
10
730
930
1130
1330
1530
1730
HOUR INTERVAL

indicating the importance of the daily change of environmental temperature in the field. Berk and Heath (1975b) concluded that the high and low temperature set point mechanisms behaved independently. Field results for *Cyclura* do not agree with this. Nonetheless, the capability for independent change probably does exist in *Cyclura*.

The highest recorded maximum T_b's for individual lizards were not significantly correlated with their lowest recorded minimum T_b's (Figure 22: Y = 0.259 X + 32.4, X = Y at 43.7 C, r = 0.290). However, the means of the daily maximum T_b's were highly and directly correlated with the means of the daily minimum T_b's for individual lizards in the population sample (Y = 0.802 X + 8.8, X = Y at 44.4 C, r = 0.970). Two lizards were excluded from the latter regression line calculation: a male which still shuttled at a low rate after four days in the thermal gradient, and Lizard 4, a caged, recently spent female which exhibited nest defense behavior, staying in her burrow much of the time except to rush at approaching free-ranging males and females outside her cage. The minimum and mean of minima increased more rapidly than the maximum and mean of maxima as T_b increased, resulting in both regression lines extrapolating to X = Y lines of perfect thermoregulation at 43.7 and 44.4 C, respectively, approximately equal to the highest maximum voluntary tolerance recorded, 43.8 C.

Regression lines were calculated for daily maximum vs. daily minimum T_b's and mean of daily T_b maxima vs. mean of daily T_b minima for individual lizards monitored a sufficient number of days (Table 10). Two-thirds of the maximum vs. minimum T_b correlations were significant, in contrast to the population sample analysis (Figure 22). Only three X = Y values, for Lizards 3, 8, and 6, were quite far removed from 43.8 C, the maximum

Figure 22. Correlations of the maximum vs. minimum T_b and the mean of T_b maxima vs. minima for individual lizards. Each point represents the results for a single lizard monitored over several days. Solid and dashed lines encompass minimum-maximum and mean of minima-mean of maxima correlations, respectively. The horizontal dotted line indicates the highest voluntary T_b recorded for *Cyclura* (43.8 C). The r values were 0.290 ($p > 0.05$) and 0.970 ($p \leq 0.0005$) for the minimum-maximum and mean of minima-mean of maxima correlations, respectively. Lizards monitored in the thermal gradient are represented by open triangles, lizards monitored in the field in February by solid dots, June-July by solid triangles, August-September by solid squares, and October by open circles. The two values marked by asterisks were not included in the regression line calculation of the mean of minima-mean of maxima correlation. See text for an explanation.

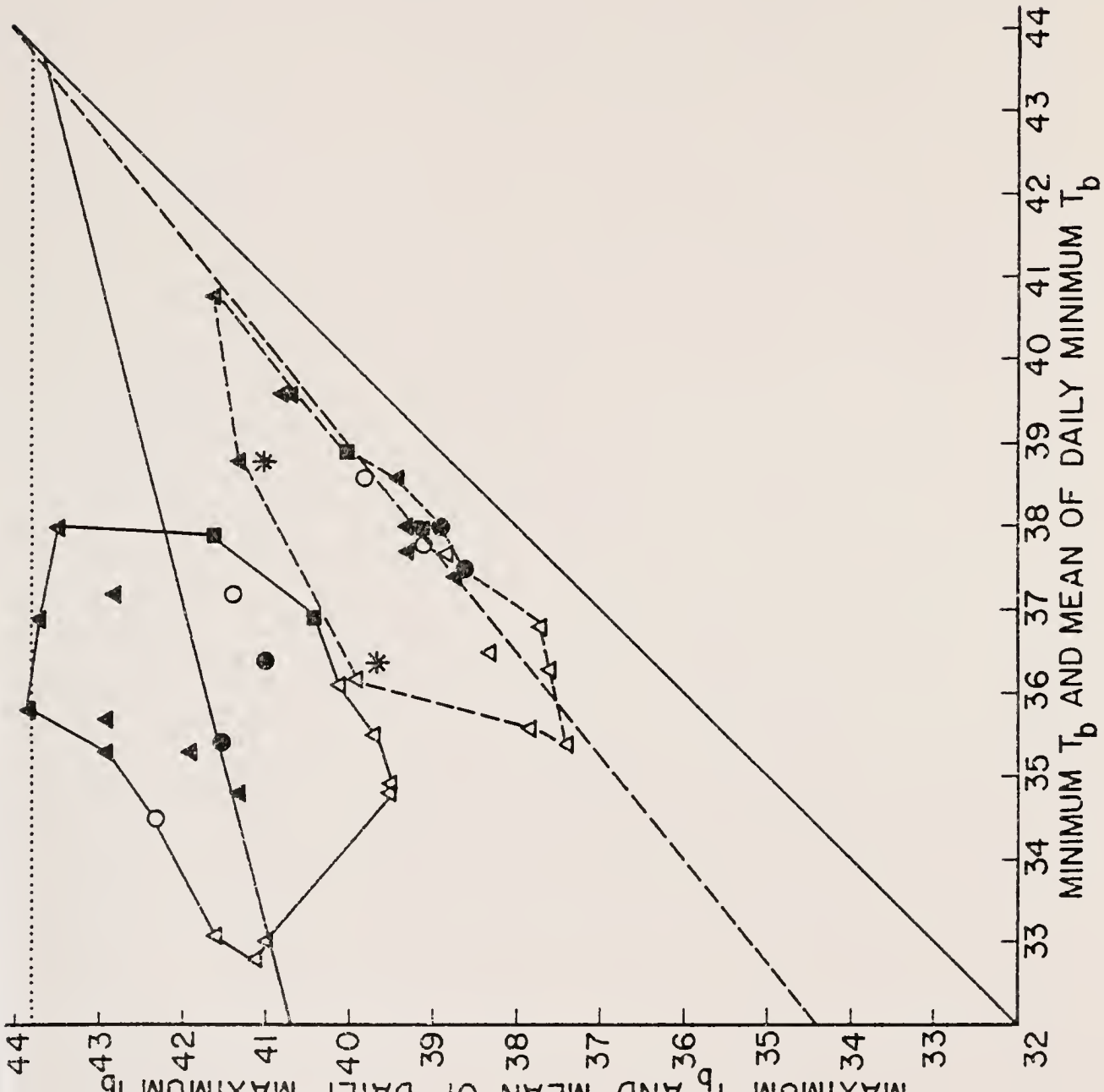

MAXIMUM T_b AND MEAN OF DAILY MAXIMUM T_b
MINIMUM T_b AND MEAN OF DAILY MINIMUM T_b
44
43
42
41
40
39
38
37
36
35
34
33
32
33
34
35
36
37
38
39
40
41
42
43
44

Table 10. Linear regression analysis of daily minimum vs. daily maximum T_b's and mean of daily T_b minima vs. mean of daily T_b maxima for individual lizards.

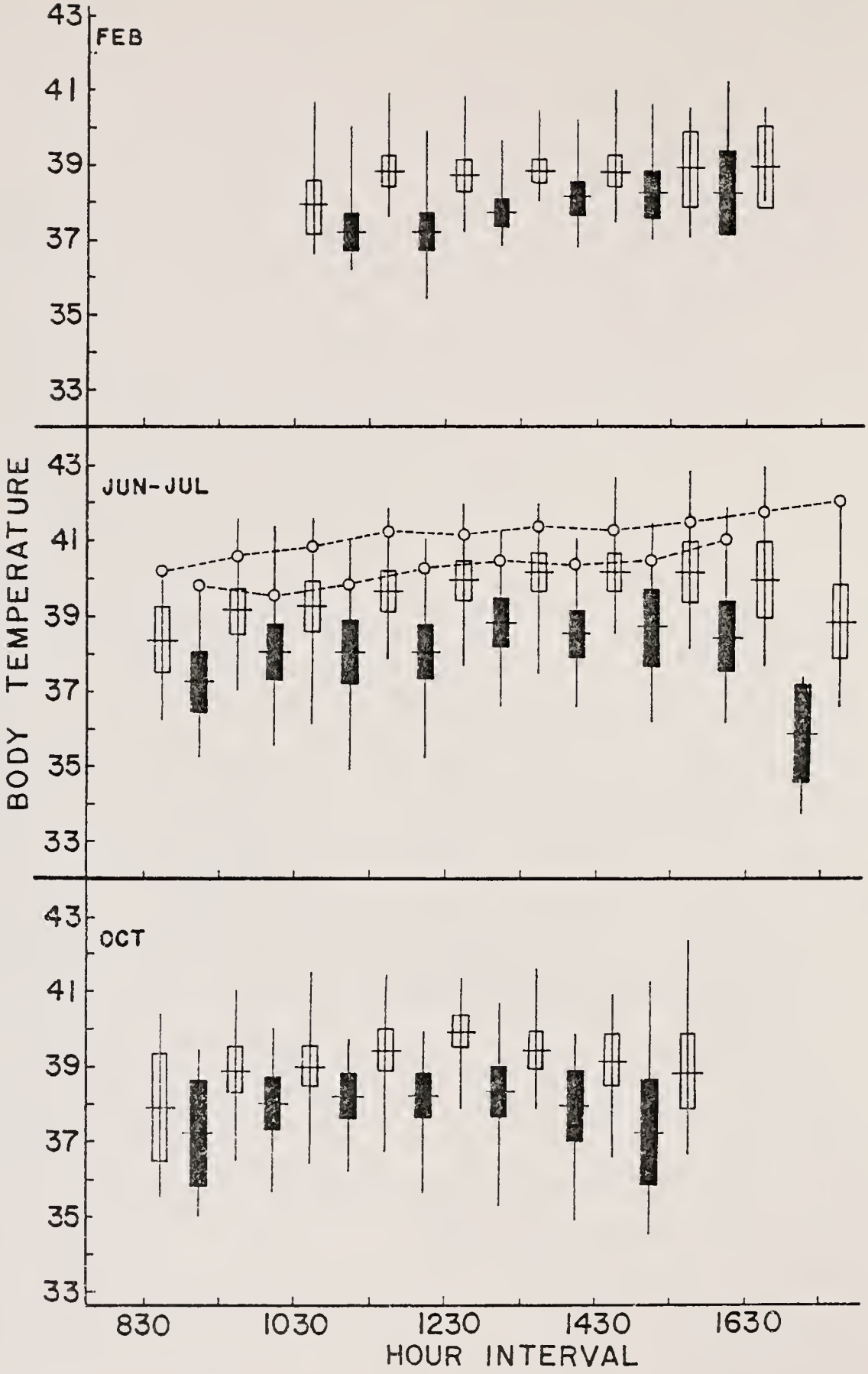
LIZARD	2	3	8	9	10	11	3	3	4
CONDITION	Free-Ranging	FR	FR	FR	FR	FR	FR	Gradient	C
MONTH	Feb	Feb	June	June	July	July	Oct	Jan	Jan
T_B RANGE	4.6	5.2	5.5	5.5	7.9	7.9	7.8	4.0	4.5
N (DAYS)	7	7	8	12	10	12	11	8	9
				DAILY MINIMUM T_B (X) VS. DAILY MAXIMUM T_B (Y)					
SLOPE	0.041	0.992	0.808	0.652	0.466	0.558	0.702	0.414	0.881
INTERCEPT	37.7	2.8	10.2	16.1	23.5	19.5	14.2	24.0	6.8
X = Y	39.4	353.3	53.3	46.4	44.0	44.1	47.6	40.9	57.1
r	0.066	0.890	0.875	0.775	0.470	0.923	0.815	0.507	0.741
P	NS	0.005	0.005	0.005	NS	0.0005	0.005	NS	0.025
				$\bar{X}$ OF DAILY T_B MINIMA (X) VS. $\bar{X}$ OF DAILY T_B MAXIMA (Y)					
SLOPE	0.877	0.912	1.059	0.874	0.710	0.912	0.661	0.592	0.811
INTERCEPT	5.45	4.3	-1.1	5.9	12.4	4.2	14.0	16.5	7.9
X = Y	44.3	48.6	19.0	46.9	42.9	48.3	41.3	40.5	41.6
r	0.850	0.969	0.917	0.981	0.954	0.973	0.877	0.834	0.929
P	0.01	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.005	0.0005

voluntary tolerance recorded for *Cyclura*. The correlations of the mean of the daily maxima vs. mean of the daily minima were all significant. Only Lizard 8's X = Y value greatly differed from 43.8 C. Thus, if the sample of monitoring days is fairly large for each lizard, the daily mean of maxima vs. mean of minima lines usually have similar slope and lesser length than the dashed line of Figure 22. The position of a lizard's line along the population line varies with season, vegetational density and height of the habitat, reproductive state of females, and, perhaps, the level of social dominance of males.

The pattern of hourly change of maximum and minimum T_b differed seasonally (Figure 23). The hourly maximum recorded T_b at both Sites I and II and the mean hourly maximum T_b at Site I were highest late in the summer afternoons, long after air and substrate temperatures passed their maxima. T_b increased until late in the day in 61 percent of the summer lizard days monitored (last maximum T_b minus first maximum = 0.5-3.0 C, $\bar{X}$ = 1.7, SD = 1.0), remained essentially level in 31 percent, and trended downward in only 8 percent (the maximum). Mean hourly maximum T_b shifted to midday in October, but a large male still occasionally reached maximum T_b during late afternoon basking (3 of 13 fair weather records). Half of all daily maxima still occurred after 1500 in February, although a levelling off of daily body temperature variation had occurred.

The timing of the maximum daily T_b for four summer and four winter acclimatized lizards gradually shifted to the final hour of the photophase in the thermal gradient, even though photophase air and substrate temperatures were fairly constant after an initial four hour increase

Figure 23. Hourly change in minimum and maximum body temperatures. Each month's sample consists of two free-ranging lizards monitored for several days. Mean minimum and mean maximum T_b's for June sample are indicated by open circles and are connected by dashed lines. Means for the other months' samples are indicated by horizontal lines. Vertical lines are ranges, open and solid rectangles are plus and minus two standard deviations of the mean for hourly minimum and maximum T_b's, respectively. June data were collected at Site I, all other data at Site II. Cloud-caused minima and maxima were excluded from the calculations.


FEB
JUN-JUL
OCT
43
41
39
37
35
33
BODY TEMPERATURE
830
1030
1230
1430
1630
HOUR INTERVAL

(Figure 24). The standard deviation of the mean time on the fourth day was one-third that of the first day. The daily maximum T_b remained during the last hour in two lizards monitored an additional four days. Thus, a unimodal timing pattern for daily maximum T_b's was clear in both field and gradient. *Cyclura* appears to become more tolerant of high body temperatures as time progresses toward the late afternoon, when overheating in direct sunlight is less likely or impossible. Concurrently, the mean time of the daily minimum T_b shifted toward midday in the thermal gradient, but without a corresponding reduction in the standard deviation.

The timing pattern of minimum T_b's was less clear in both free-ranging and gradient lizards. Hourly frequency distributions of the daily minimum T_b were weakly bimodal in June, July, and October, with the expected dip during the hottest part of the day. The pattern was reversed in February, with the majority of the daily minima occurring near midday. The reason for this seasonal difference is unknown.

Caged summer lizards had a different pattern than free-ranging summer lizards in their hourly frequency distributions of T_b minima and daily minimum T_b's. In the caged summer lizards, both frequency distributions peaked unimodally between 1100 and 1200, an hour before the maximum depression in the core T_b's at shade seeking and sun seeking (see Figure 46 and corresponding text). The number of hourly T_b minima for summer free-ranging lizards did not vary much between 1000 and 1600 and, as stated above, the hourly distributions of daily minimum T_b's were weakly bimodal. These two differences between caged and free-ranging lizards are probably related to the harsher thermal environment of the cages, especially around midday. Barber and Crawford (1979)

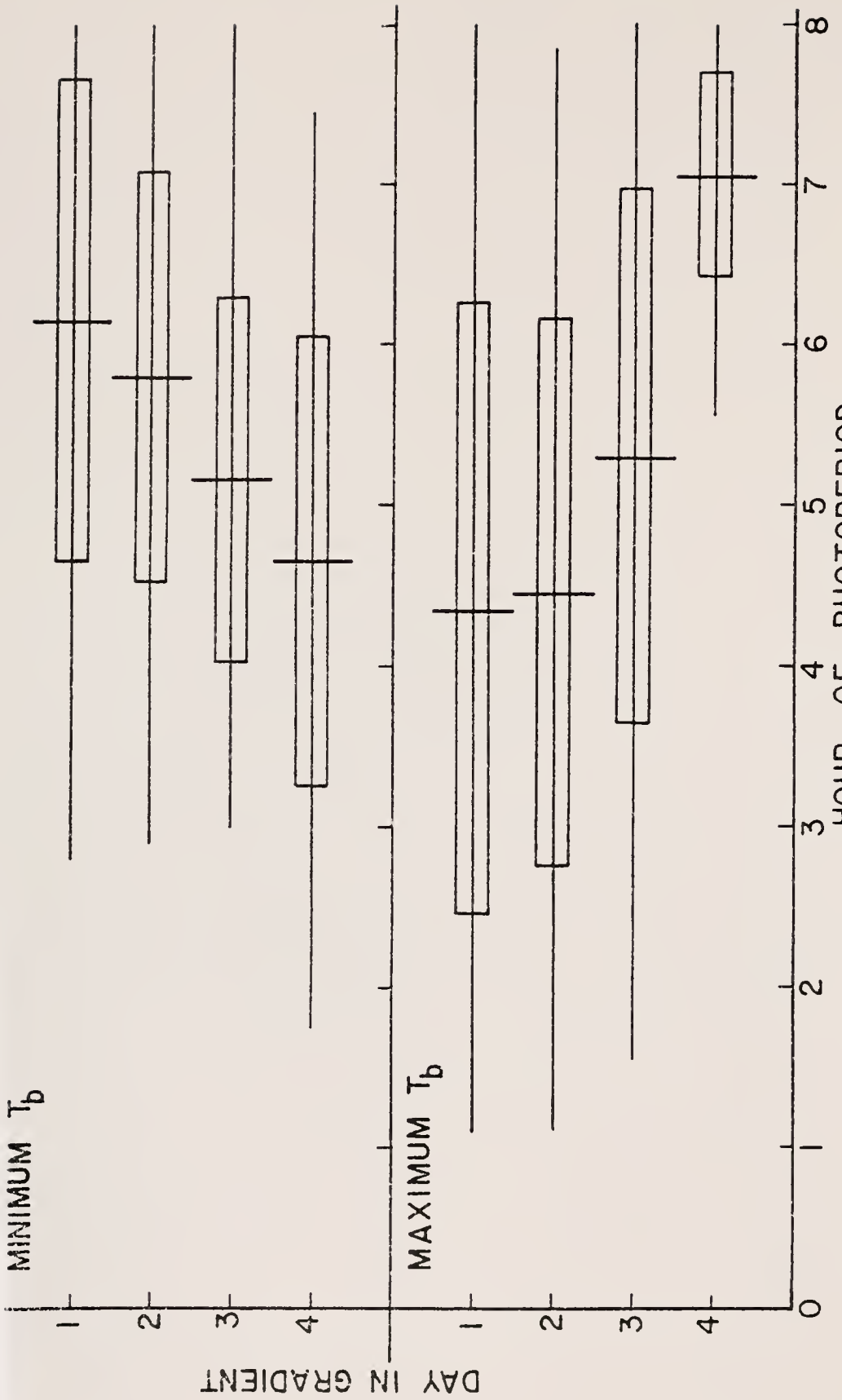


Figure 24. Timing shift of daily minimum and maximum T_b's. Eight lizards, half acclimatized to summer and half to winter conditions in Gainesville, were monitored during their first four days in the thermal gradient. Horizontal lines are ranges, vertical lines are means, and rectangles are plus and minus two standard errors of the mean.

found that as the hot environment temperature in a two-chambered gradient increased, the colonic temperature of *Dipsosaurus* at exit from the heat decreased, similar to the caged *Cyclura*. However, the maximum dorsal subsurface temperature remained constant. Thus, the subsurface temperature appeared to be more important in controlling the timing of shuttling away from the heat than the core temperature. The midday depression in core temperature may simply be the result of the greater temperature lag expected between surface and core in a more rapidly heating animal. The panting setpoint showed a similar midday depression in caged lizards (see Figure 58 and corresponding text), indicating that it also may be controlled by a skin input.

Skewness of Body Temperature Frequency Distributions

Cyclura field and gradient T_b distributions both trended slightly toward negative skewness (Table 11). The test statistic used was a_3 (Remington and Schork 1970); positive and negative values resulted from positive and negative skew, respectively. Eight of ten significantly skewed distributions were negative, equally distributed between field and gradient. The trend was about equal in both locations. Antipodal results for different lizards were evident in all seasonal samples, especially in the field in February and in the gradient in July-August.

The test statistic a_4 (Remington and Schork 1970) was used to determine the degree of kurtosis in the T_b frequency distributions (Table 11). Kurtosis could be tested for in samples of 50 or more (Pearson and Hartley 1966, Table 34, p. 208). Values significantly less than three indicate the distribution is platykurtic, significantly greater than three; leptokurtic, and not significantly different from

Table 11. Skewness and kurtosis of T_b frequency distributions. Data points (N) were taken from the T_b records at 15 minute intervals for a variable number of monitoring days. C and FR stand for free-ranging and caged, respectively. T_b's during extended overcast periods were not included. Only third and fourth day monitoring results were used for the thermal gradient calculations. See the text for an explanation of the statistical tests.

FIELD									
				SKEWNESS				KURTOSIS	
MONTH	CONDITION	DAYS/N	$\bar{X}$ T_b	(a_3)	P	MONTH	LIZARD	(a_4)	P
Aug	12(FR)	4/44	39.5	-1.329	0.01	Aug	12	4.911	0.05
Feb	2(FR)	7/130	38.2	-0.848	0.01	Feb	2	4.001	0.05
Feb	1(FR)	3/48	37.8	-0.718	0.05	Feb	1	3.117	NS
Jun	9(FR)	8/236	41.3	-0.684	0.01	Oct	2	3.009	NS
Jun	4(C)	5/109	40.1	-0.322	NS	Feb	3	2.996	NS
Oct	14(FR)	3/54	39.6	-0.240	NS	Jun	4	2.880	NS
Jun	6(C)	5/114	37.9	-0.206	NS	Oct	14	2.871	NS
Oct	2(FR)	4/66	39.3	-0.179	NS	Jun	6	2.830	NS
Jul	11(FR)	10/283	40.1	-0.056	NS	Jul	10	2.737	NS
Jun	7(C)	7/194	38.7	-0.018	NS	Jun	5	2.661	NS
Jun	5(C)	6/177	40.3	-0.016	NS	Sept	13	2.572	NS
Jul	10(FR)	7/199	38.9	-0.008	NS	Jun	9	2.481	0.05
Oct	15(FR)	3/58	39.2	-0.002	NS	Jun	7	2.442	0.05
Oct	3(FR)	9/196	38.8	+0.105	NS	Jun	8	2.356	0.05
Sept	13(FR)	5/81	38.5	+0.209	NS	Oct	3	2.228	0.01
Jun	8(FR)	7/165	40.3	+0.234	NS	Oct	15	2.132	0.05
Feb	3(FR)	6/143	38.4	+0.865	0.01	Jul	11	1.778	0.01
			$\bar{X}$ (SD)	-0.189(0.497)			$\bar{X}$ (SD)	2.824(0.725)	
THERMAL GRADIENT									
Jul	5	2/56	37.5	-0.904	0.01	Jul	3	5.766	0.01
Dec	1	2/37	36.8	-0.687	0.05	Jan	4	3.344	NS
Aug	7	2/55	37.3	-0.503	0.05	Jul	5	3.143	NS
Aug	6	2/57	35.8	-0.500	0.05	Aug	6	2.751	NS
Jan	3	2/51	38.0	-0.423	NS	Aug	7	2.642	NS
Dec	2	2/34	35.8	-0.030	NS	Dec	1	2.593	--
Jan	4	2/52	37.1	+0.258	NS	Jan	3	2.557	NS
Jul	3	2/53	37.0	+0.908	0.01	Dec	2	2.298	--
			$\bar{X}$ (SD)	-0.235(0.588)			$\bar{X}$ (SD)	3.137(1.114)	

three; mesokurtic or similar to the normal distribution. The field distributions trended toward platykurtosis (six platykurtic and two leptokurtic distributions) whereas gradient distributions did not.

The T_b distributions of the field lizards monitored in the summer were examined on a day by day basis to see if skewness changed in a consistent way with increasing daily mean T_b (Figure 25). The trend toward negative skewness was most evident in the midrange of mean T_b. As expected, positive skewness predominated in the T_b distributions of hyperthermic lizards. However, the expected predominance of negative skewness at low mean T_b's was not present. Clearly, the overall divergence of distributions from normality was small, since only 7 of 52 distributions or 13.5 percent were significantly skewed.

The mean and standard deviation adequately describe a lizard's body temperature frequency distribution only if the distribution is normal. Since distributions were negatively skewed in *Dipsosaurus dorsalis* monitored in a continuous gradient, DeWitt (1967) substituted the median and the central 50, 68, and 95 percent of the total observations to describe the level and precision of thermoregulatory control, respectively. Figure 26 compares the level and precision of thermoregulation of *Cyclura* and *Dipsosaurus*, two fairly closely related herbivorous iguanines. Median T_b of the desert iguana was approximately 1.5 C above the rock iguana (upper graph), probably due to the more thermally extreme habitat of the desert iguana. The medians of the three samples have been superimposed in the lower graph, allowing comparisons of relative thermoregulatory precision. Negative skewness was expressed at each of the three central percentages in *Dipsosaurus*, whereas

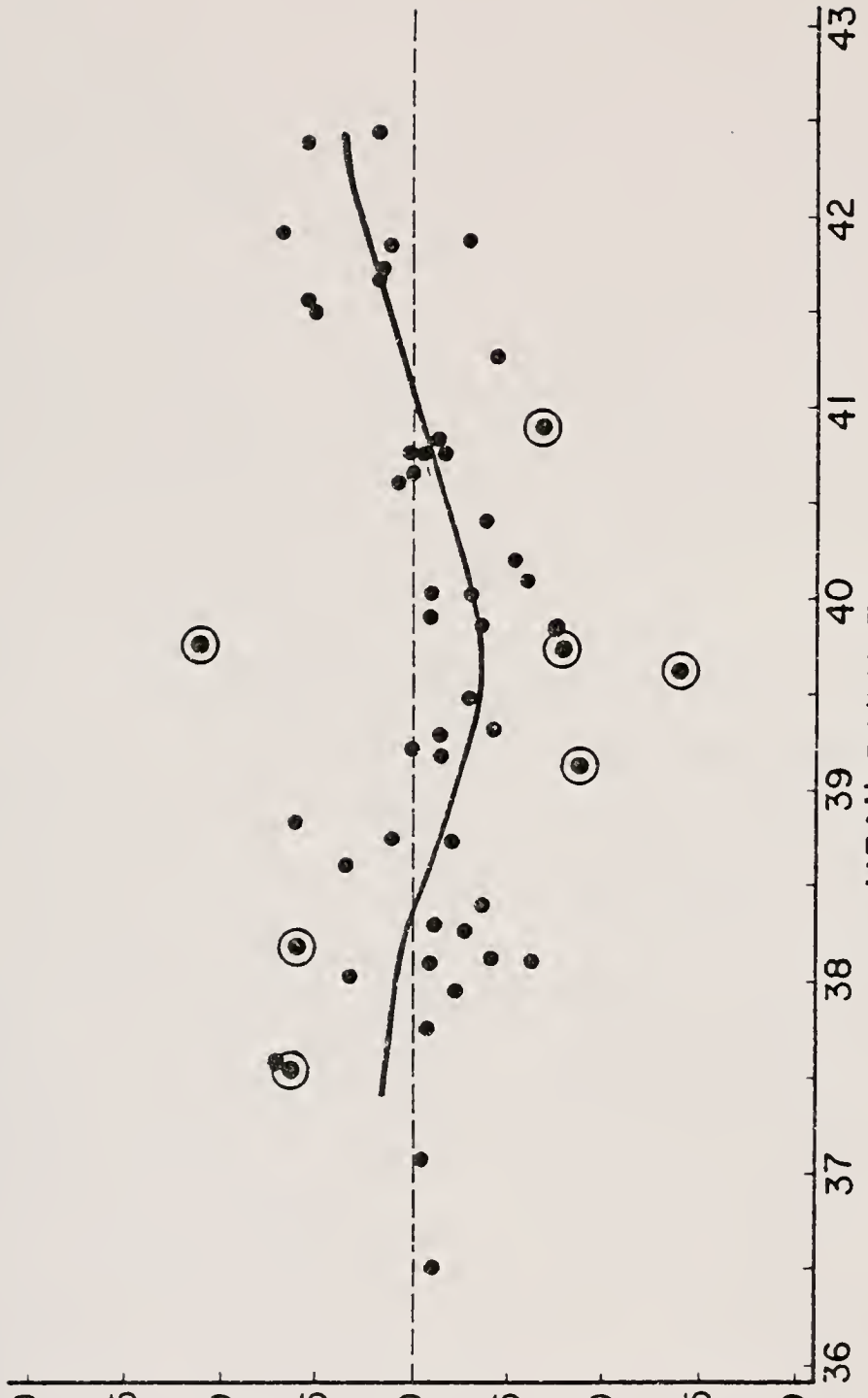


Figure 25. Skewness of daily T_b frequency distributions. The sample consisted of four caged and four free-ranging lizards monitored in June or July. Circled dots are a_3 values for distributions with significant positive or negative skew ($p < 0.05$). The curve follows the mean a_3 values for the mean T_b of each 1 C interval. Days with extensive cloud cover were omitted from the analysis. Hyperthermic lizard a_3 values were included.

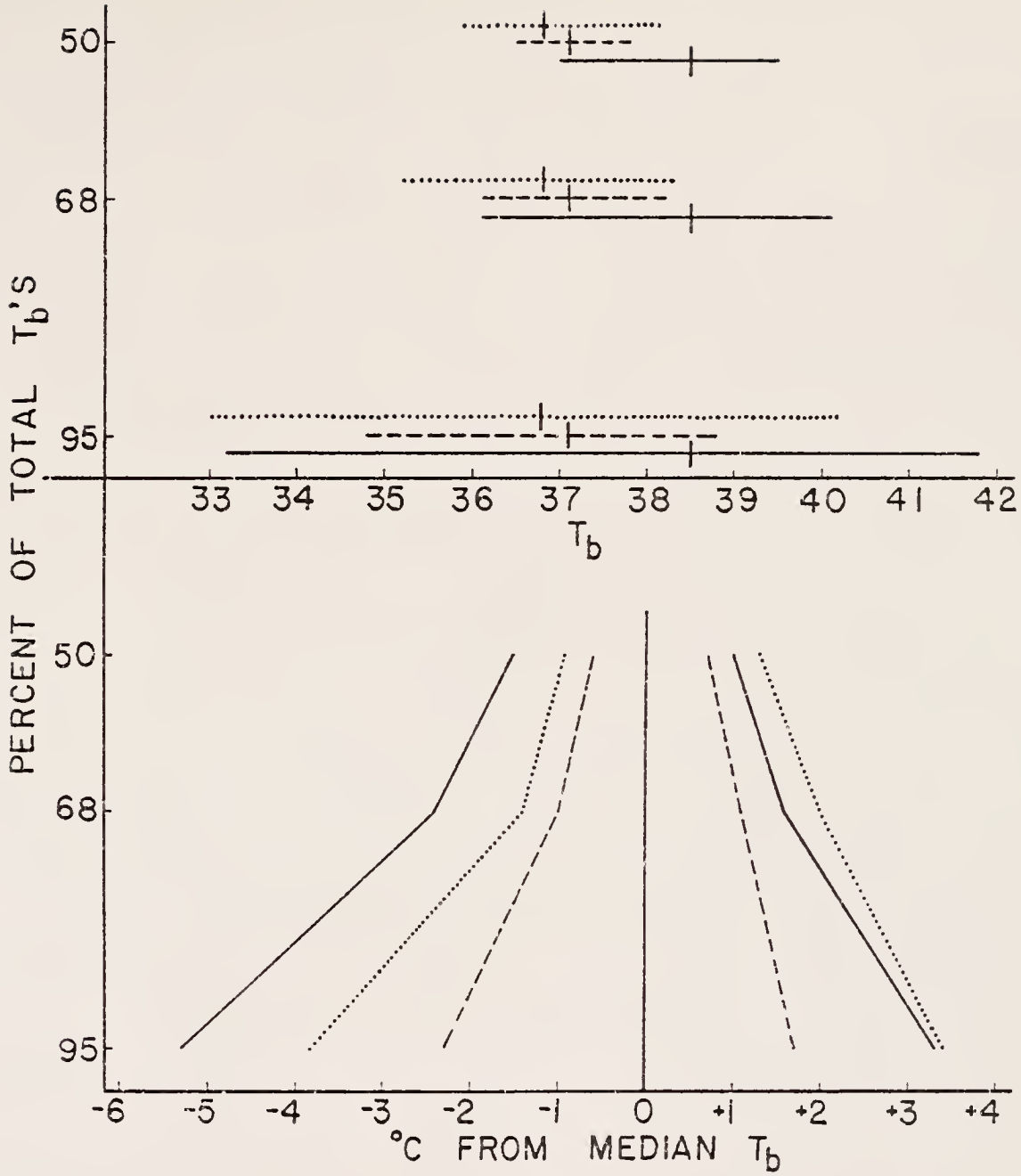


Figure 26. Comparison of the level and precision of thermoregulation of *Cyclura carinata* and *Dipsosaurus dorsalis* in continuous thermal gradients. *Cyclura* data were obtained from four lizards monitored on the third and fourth days in July-August (dotted lines) and third to fifth days in December-January (dashed lines), *Dipsosaurus* data (DeWitt 1967) from 11 individuals monitored for three days (solid lines). Horizontal lines are ranges encompassing 50, 68, and 95 percent of the regulating phase T_b's. Vertical lines are median T_b's.

the *Cyclura* distributions were negatively skewed only when 95 percent of the observations were included. *Cyclura*'s precision was greater than *Dipsosaurus* below the median, but only for the winter sample above the median. The greater thermoregulatory precision of the rock iguana may be partially due to its larger body size, resulting in lower heating and cooling rates. Unfortunately, the validity of the species comparison is impaired by the differing sample sizes, the use of different kinds of continuous thermal gradients, and acclimatization of lizards to different thermal environments prior to testing.

Standard Deviation of Mean Body Temperature

The standard deviation decreased as mean T_b increased (Figure 27), in agreement with the maximum vs. minimum T_b and mean of maxima vs. mean of minima correlations previously described. The correlation was not significant for the February data. The regression lines extrapolated to zero SD at 45.2 C mean T_b (February), 45.9 C (June-July), and 43.8 C (October), again similar to the previously described results. Since mean T_b was inversely related to the total overcast time per day, a multiple linear regression analysis for trivariate data was run to determine the relative importance of overcast time and mean T_b on the SD. The results indicate that overcast time (T_o, in minutes) was unimportant as a correlate of the SD (February: SD = 11.201 - 0.272 $\bar{X}_{T_b}$ - 0.001 T_o; June-July: SD = 8.406 - 0.191 $\bar{X}_{T_b}$ + 0.010 T_o; October: SD = 6.328 - 0.143 $\bar{X}_{T_b}$ + 0.001 T_o).

A large lizard should have a lower SD of mean T_b than a small lizard, even when their means of maxima and minima are identical, due to the higher heating and cooling rates of the smaller lizard. *Cyclura*

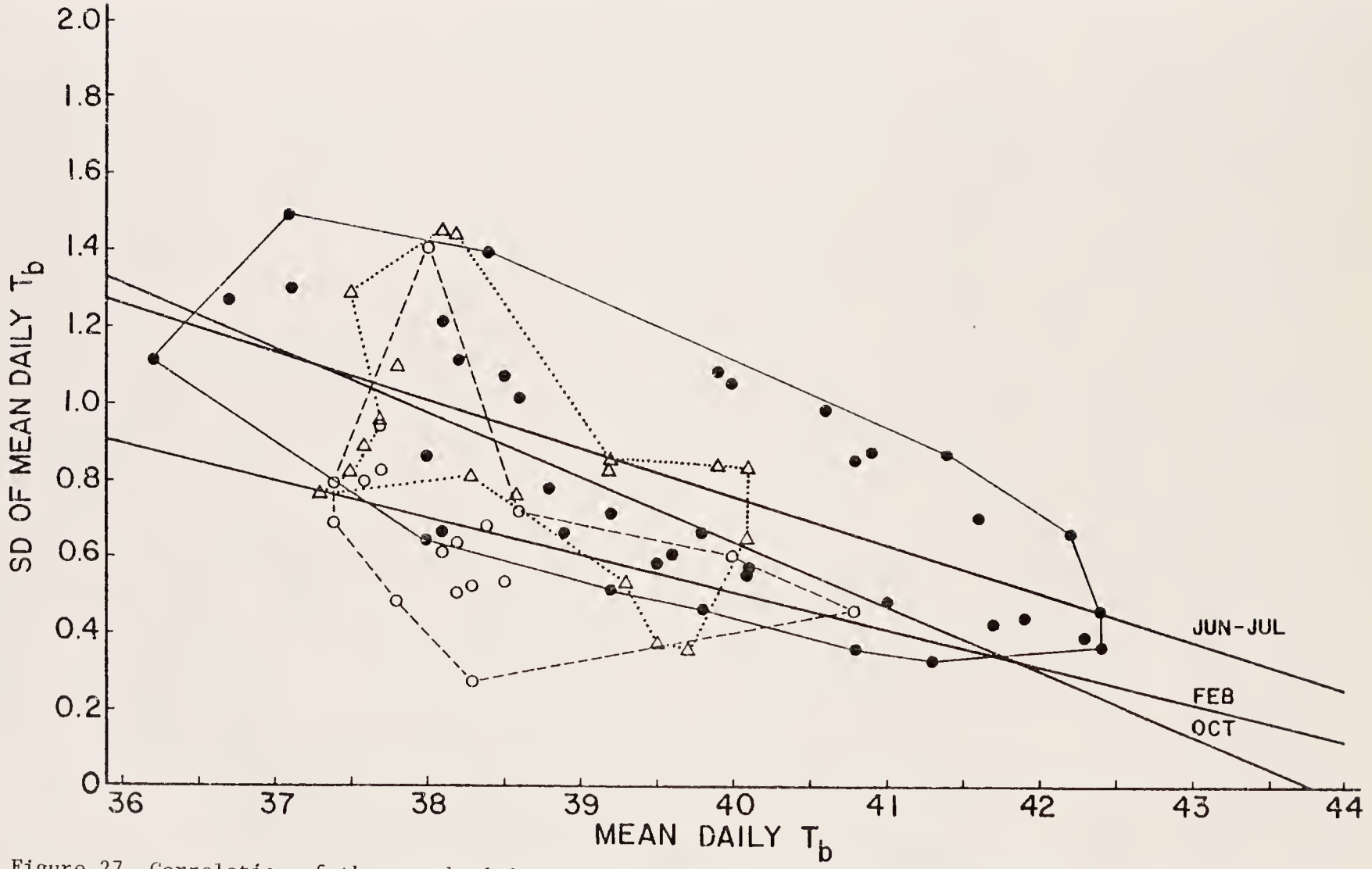


Figure 27. Correlation of the standard deviation of mean daily T_b with mean daily T_b. Data are from free-ranging lizards in February (open circles, dashed line), June-July (solid circles and line), and October (open triangles, dotted line). Monitoring days with long overcast periods were excluded. Correlation coefficients for the regression lines were 0.345 (February, $p > 0.05$), 0.688 (June-July, $p \leq 0.0005$), and 0.535 (October, $p \leq 0.01$).

has a large ontogenetic weight range. However, I monitored the T_b of only one small individual, weighing 180 g (approximately three years old). Thus, summer lizards could be lumped into only two weight classes, with means of 729 and 1446 g (Figure 28). The smaller lizards had a higher mean SD at all mean T_b intervals, but the differences were not significant. The equation resulting from a multiple linear regression analysis of the summer field data was: $SD = 10.02 - 0.217\ \bar{X}_{T_b} - 0.0004\ W_b$. Thus, for example, the influence of mean T_b on the SD was 12.9 times greater than body weight for a 1600 g *Cyclura* with a mean T_b of 38 C.

The inverse relationship between the SD and $\bar{X}\ T_b$ still held when examined on an hourly basis (Figure 29). Early morning heating and late afternoon cooling just prior to and after submergence resulted in the greatest SD's, due to the rapid rates of T_b change and the day to day individual variation in times of emergence and submergence. The female Lizard 8 and the subdominant male Lizard 10 submerged earlier than the dominant males 9 and 11, usually still emergent through the final time interval illustrated in the graphs. In contrast to the inverse relationship of the SD and lizard mean T_b, the SD's and the means of shaded air and sand temperatures at ten different sites varied directly. A lizard had the greatest diversity of shade temperatures to choose from during the hottest part of the day. Of course, some of these shaded environments were unsuitably warm. *Cyclura* was quite selective in choosing its shade, especially during the hottest part of a summer day when a large portion of the habitat was too hot for the lizard to remain in for long.

Figure 28. Effect of body weight and mean T_b on the standard deviation of mean T_b. The sample consisted of eight summer field lizards, five in a low weight group ranging from 645 to 815 g and three in a high weight group ranging from 1290 to 1598 g. Vertical lines are ranges, horizontal lines are means, and rectangles are plus and minus two standard errors of the mean.

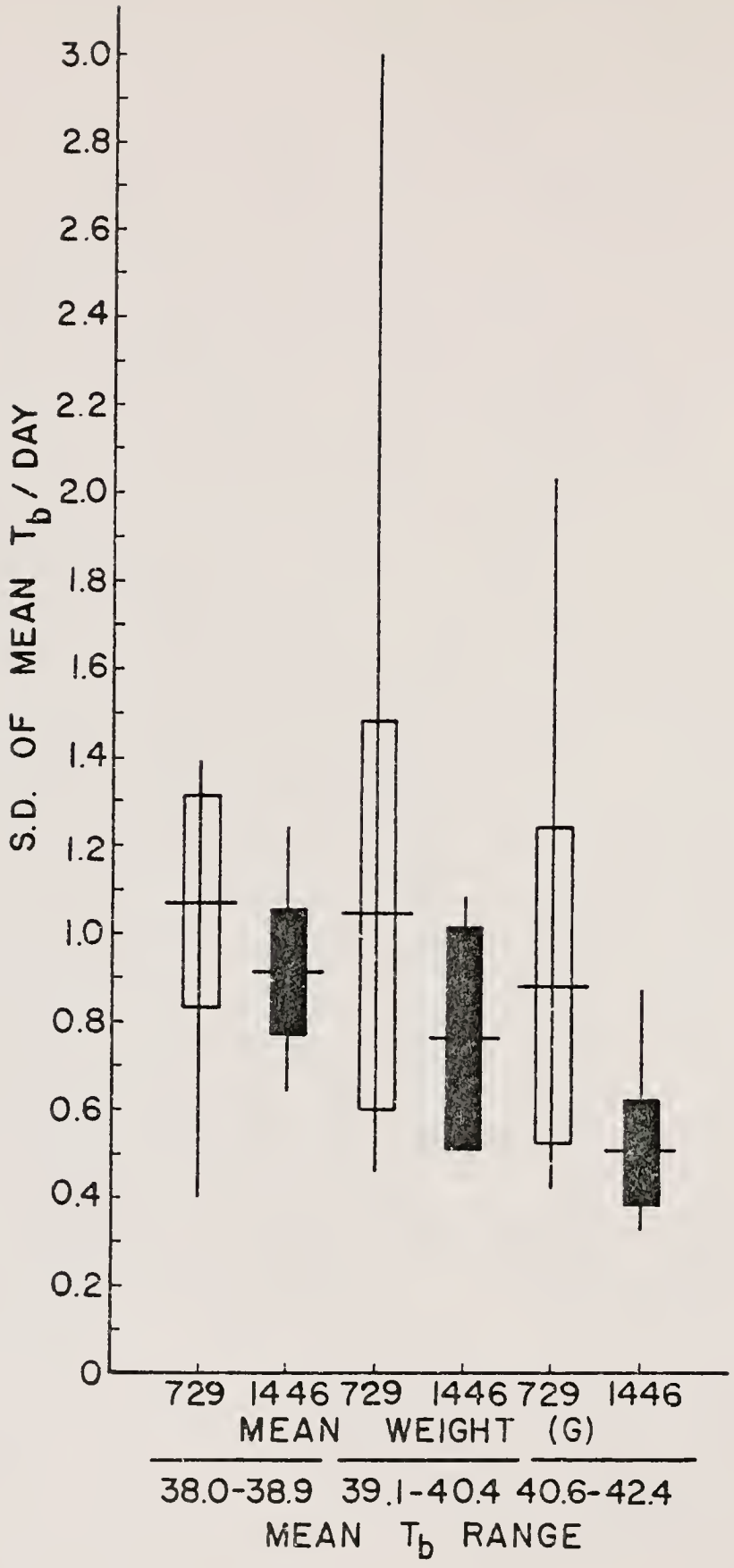
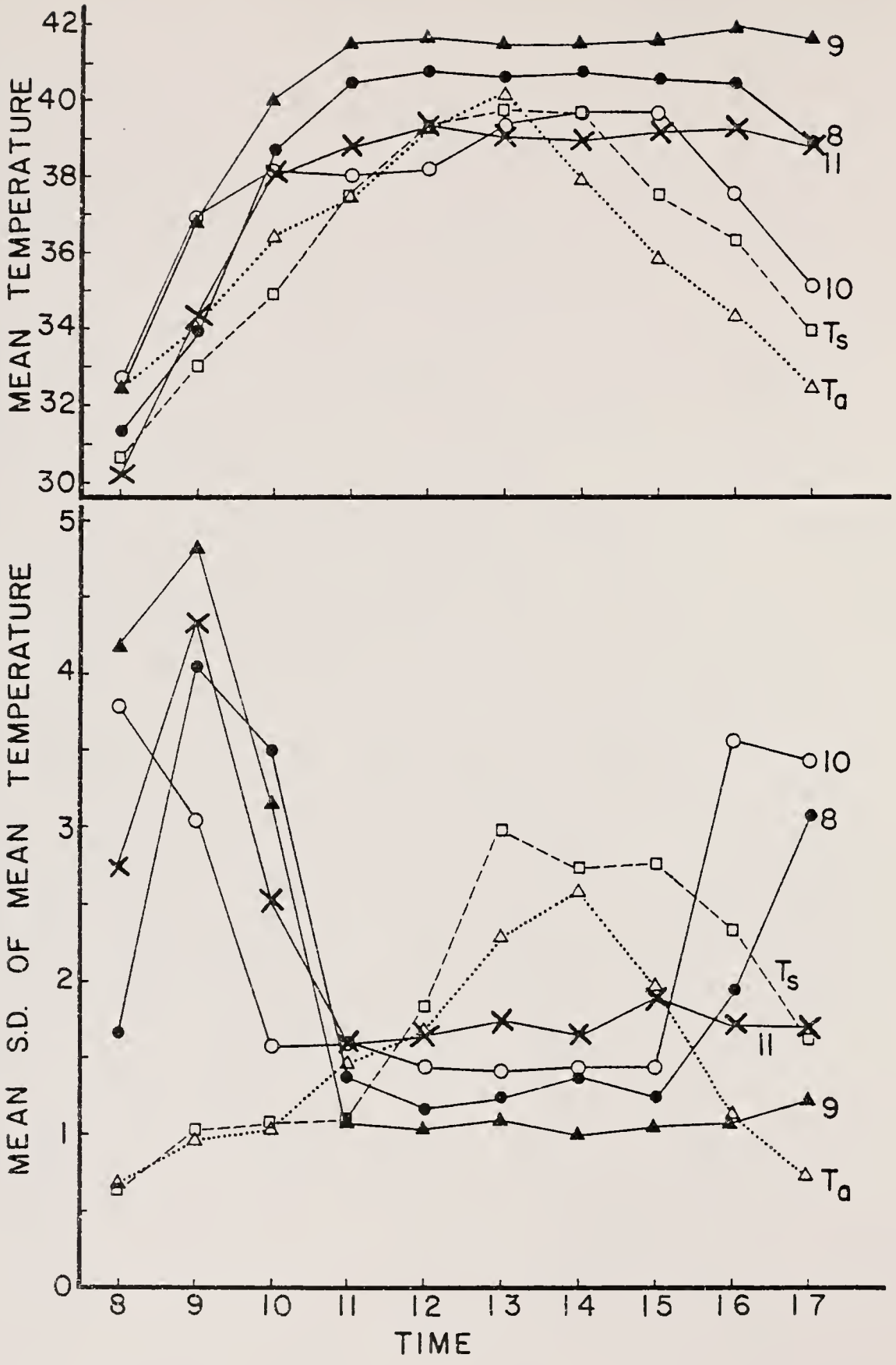

S.D. OF MEAN T_b / DAY
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
729 1446 729 1446 729 1446
MEAN WEIGHT (G)
38.0-38.9 39.1-40.4 40.6-42.4
MEAN T_b RANGE

Figure 29. Hourly change in the mean and standard deviation of lizard body temperature and shaded air and sand temperatures. The highest and lowest T_b's recorded each hour of each day (0730-0829, 0830-0929, etc.) were used to calculate the mean T_b and standard deviation (8, 9, 9, and 12 monitoring days in June-July for Lizards 8-11, respectively). T_a at a height of 2 cm and T_s were measured on the hour during three days in August in the shade of ten shrubs chosen at approximately equal intervals along a 200 m line at Site I.


MEAN TEMPERATURE
42
40
38
36
34
32
30
9
8
11
10
Ts
Ta
MEAN S.D. OF MEAN TEMPERATURE
5
4
3
2
1
0
10
8
Ts
11
9
Ta
8
9
10
11
12
13
14
15
16
17
TIME

It is interesting to speculate on what determines the mean, long term, operant temperature of a heliothermic lizard which remains emergent all day. The most likely choice is the mean of all the shade temperatures possibly encountered by the lizard during the hottest part of the day of the hottest part of the year. This is substantiated somewhat by the upper graph in Figure 28. Huey and Slatkin (1976) reported that the mean preferred T_b of southwest U.S. desert lizard species was well correlated with mean, long term July environmental temperature.

Rates of Lizard Heating and Cooling in the Field

Morning Heating and Regulating Phases

The mean morning heating rate and the mean heating and cooling rates during the regulating phase were calculated for individual lizards using the following equation:

$$\bar{R} = \frac{\Sigma[(T_{b\ Max} - T_{b\ Min}) \cdot t^{-1} \cdot 60]}{N} \qquad (1)$$

where $\bar{R}$ is the mean rate of heating or cooling (C/hr), t is time (min), and N is the number of increasing or decreasing temperature periods in the sample. The slight differences in the T_b ranges of $T_{b\ Max} - T_{b\ Min}$ were ignored. The mean regulating phase heating rate exceeded the cooling rate in nine out of twelve lizards, with a mean cooling/heating ratio of 0.87 (Table 12). However, none of the ratios were significantly different from one ($p > 0.05$).

On the average the mean morning heating rate was 3.3 and 4.0 times greater than the mean regulating phase heating and cooling rates,

Table 12. Rates of lizard heating and cooling in the field during the morning heating and regulating phase.

		MORNING HEATING PHASE				
LIZARD/ MONTH	WEIGHT (G)	N (DAYS)	$\bar{X}$ RATE (C/HR)	SD	LOW/HIGH	$\frac{1}{2}$
2/Feb	1665	8	11.2	1.9	9.1/14.9	4.1
3/Feb	1775	6	10.3	3.1	7.6/15.0	3.1
4/June	645	3	11.0	-	6.0/21.0	1.8
5/June	723	-	-	-	-	-
6/June	815	7	7.3	1.5	5.4/9.1	3.5
7/June	1290	3	6.7	-	6.1/7.3	1.4
8/June	675	6	11.0	4.0	6.4/16.9	3.0
9/June	1450	11	8.7	1.8	5.0/11.6	5.1
10/July	787	8	9.6	3.1	5.8/14.6	3.1
11/July	1598	16	8.4	2.2	5.8/14.6	3.8
13/Sept	950	5	11.6	4.0	8.9/18.5	4.6
3/Oct	1672	10	7.8	2.3	5.6/12.0	3.0
		$\bar{X}$	9.4			3.3
		SD	1.7			1.1

Table 12. Continued.

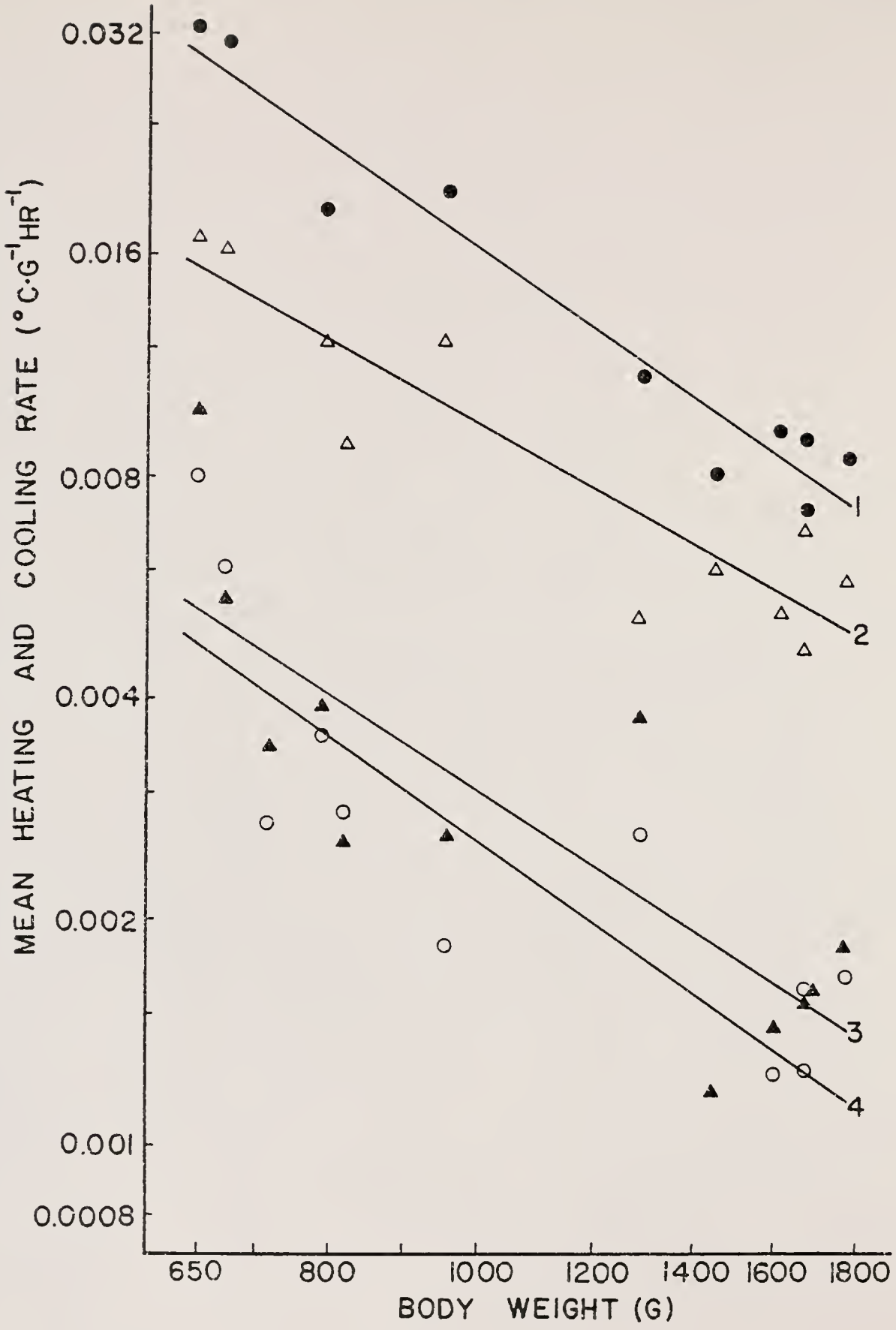
REGULATING PHASE								
HEATING				COOLING				
N/5 DAYS	$\bar{X}_2$ RATE (C/HR)	SD	LOW/HIGH	N/5 DAYS	$\bar{X}_3$ RATE (C/HR)	SD	LOW/HIGH	$\frac{3}{2}$
28	2.7	1.9	0.4/9.5	28	2.1	1.3	0.6/6.0	0.76
31	3.3	3.1	0.7/13.2	31	3.0	2.1	0.6/8.0	0.90
22	6.0	4.4	0.8/14.0	22	5.2	3.6	1.3/12.4	0.88
29	2.5	1.9	0.2/7.5	29	2.0	1.5	0.4/7.3	0.79
20	2.1	1.2	0.2/4.5	20	2.3	1.7	0.4/6.4	1.06
27	4.9	3.7	0.7/14.2	27	3.4	3.7	0.4/18.0	0.76
29	3.7	4.0	0.2/21.0	29	4.1	4.1	0.4/14.4	1.11
26	1.7	1.4	0.2/6.0	26	1.1	0.8	0.1/3.7	0.64
36	3.1	2.1	0.2/9.7	36	2.8	2.0	0.4/9.1	0.92
32	2.2	1.4	0.5/7.3	32	2.0	1.8	0.2/12.0	0.92
16	2.5	1.2	0.4/4.6	16	1.8	0.5	0.8/2.7	0.70
34	2.6	1.6	0.4/7.9	34	2.7	1.8	0.4/8.3	1.03
	3.1				2.7			0.87
	1.2				1.1			0.15

respectively (Table 12). Lizards maximized their heating rates behaviorally for a time before beginning their first long distance movements away from the home burrow in the morning. Heating and cooling during the regulating phase commonly occurred in a sun-shade mosaic under vegetational cover. Various thermoregulatory behaviors, described later, were intermittently in force during both regulating phase heating and cooling. Low rates of regulating phase heating and cooling were attained for short periods by every lizard in the sample, since numerous shaded areas were contained in every home range.

The rates of heating and cooling decreased as body weight increased, due to the decrease in surface to volume ratio. Plots of the logs of weight specific rates of maximum recorded heating, mean morning heating, and mean regulating phase heating and cooling vs. the log of body weight were linear, and the slopes were approximately equal (Figure 30). The equations, correlation coefficients, and significance levels for the regression lines were: $Y = -1.40\ X + 2.40$, $r = -0.975$, $p \leq 0.0005$ for the maximum heating rate, $Y = -1.12\ X + 1.34$, $r = -0.925$, $p \leq 0.0005$ for the mean morning heating phase rate, $Y = -1.30\ X + 1.39$, $r = -0.839$, $p \leq 0.0005$ for the mean regulating phase heating rate, and $Y = -1.41\ X + 1.65$, $r = 0.831$, $p \leq 0.0005$ for the mean regulating phase cooling rate. On the average, a doubling of body weight decreased the maximum heating rate by 62 percent, the morning heating rate by 54 percent, the mean regulating phase heating rate by 59 percent, and the mean regulating phase cooling rate by 62 percent.

The mean daily regulating phase rates of heating and cooling were directly correlated with the standard deviation of the mean daily T_b: mean daily heating rate (C/min) = 11.18 SD of mean daily T_b + 0.35,

Figure 30. Correlation of mean rates of heating and cooling in the field with lizard body weight. Regression line one represents the maximum rate of heating recorded (solid dots, one per lizard), line two; the mean rate of heating during the morning heating phase (open triangles), line three; the mean rate of heating during the regulating phase (solid triangles), line four; the mean rate of cooling during the regulating phase (open circles). Data were taken from Table 12 and transformed to weight specific rates.


0.032
0.016
0.008
0.004
0.002
0.001
0.0008
MEAN HEATING AND COOLING RATE (°C·G⁻¹HR⁻¹)
650
800
1000
1200
1400
1600
1800
BODY WEIGHT (G)
1
2
3
4

N = 43, r = 0.746, p $\leq$ 0.0005; mean daily cooling rate = 9.32 SD of mean daily T_b + 0.51, N = 43, r = 0.563, p $\leq$ 0.0005. Figure 31 summarizes the correlations between five parameters which describe regulating phase body temperatures.

Lizard Cooling in Burrows

The decline in lizard T_b during burrow cooling is best described by Newton's law of cooling:

$$\frac{dT_b}{dt} = -a\,(T_b - T_a) \tag{2}$$

Integration yields:

$$\ln(T_b - T_a) = -at + \ln(T_{bs} - T_a) \tag{3}$$

where T_b is the lizard core temperature during cooling, T_{bs} is the core temperature at submergence, T_a is the burrow air temperature at the point of the lizard, a is a cooling constant in minutes^{-1}, and t is time in minutes. By graphing t vs. $\ln(T_b - T_a)$, the slope can be calculated by linear regression and is equivalent to $-a$. Since the burrows of free-ranging lizards were not disturbed during monitoring, T_a was estimated by T_{be}, the lizard's body temperature at emergence. The equation becomes:

$$\ln(T_b - T_{be}) = -at + \ln(T_{bs} - T_{be}) \tag{4}$$

T_{be} is a good estimator of T_a since equilibrium between T_b and T_a was attained long before emergence and metabolic heat production probably caused T_{be} to be less than 2 C above T_a.

Lizard core temperature nearly equilibrated with burrow temperature after only 19 percent of the nightly submergence time (Table 13). A mean T_b decline of 10.4 C required an average of 201 minutes. The

Figure 31. Correlations of parameters describing regulating phase body temperatures.

MEAN BODY TEMPERATURE	STANDARD DEVIATION OF MEAN BODY TEMPERATURE	MEAN RATE OF HEATING	MEAN RATE OF COOLING	BODY WEIGHT
Inverse (June, July, October Only)				
None				
None				
? (Insufficient Data for Small Iguanas)				
	Direct			
	Direct			
	Inverse			
		Direct		
		Inverse		
			Inverse	

Table 13. Lizard cooling in burrows in the field. Asterisks indicate heavy rainfall during cooling.

DAY OF DATA	LIZARD	WEIGHT (G)	MONTH	BURROW LETTER CODE	T_B AT SUBMERGENCE	T_B AT EMERGENCE NEXT DAY	COOLING TIME TO $T_B - T_{BE} = 1$ C (MIN)	COOLING TIME / SUBMERGENCE TIME	COOLING CONSTANT (MIN^{-1})
1	1	1135	Feb	A	38.0	26.9	272	0.24	0.009
2	1	1135	Feb	A	39.4	26.9	284	0.26	0.009
3	1	1135	Feb	A	37.0	27.0	212	0.19	0.010
1	2	1665	Feb	B	38.7	25.9	326	0.28	0.008
2	2	1665	Feb	B	38.2	26.2	276	0.24	0.009
1	3	1775	Feb	C	38.4	27.8	251	0.24	0.010
1	8	675	June	D	39.9	29.1	148	0.14	0.016
2	8	675	June	E	42.0	28.6	140	0.13	0.018
1	9	1450	June	F	39.2	29.0	59	0.05	0.051*
2	9	1450	June	F	37.4	29.5	45	0.04	0.053*
1	10	787	July	G	39.6	30.0	224	0.22	0.009
2	10	787	July	G	39.6	30.0	174	0.17	0.013
3	10	787	July	H	39.9	28.0	316	0.33	0.008
4	10	787	July	H	37.9	28.0	242	0.20	0.009
5	10	787	July	H	40.7	29.5	210	0.20	0.011
1	11	1598	July	I	39.8	27.7	216	0.21	0.012
1	3	1672	Oct	J	36.6	29.6	147	0.14	0.011
2	3	1672	Oct	J	38.4	29.6	164	0.16	0.013
3	3	1672	Oct	A	37.8	30.2	178	0.16	0.011
4	3	1672	Oct	A	39.7	29.8	128	0.12	0.018*
				$\bar{X}$	38.9	28.5	201	0.19	
				SD	1.31	1.36	77	0.07	

cooling constant was not significantly correlated with body weight over a range of 675-1775 g (log a = -0.17 log body weight - 1.43, N = 17 days, r = -0.287, $p \leq 0.05$). Heavy rainfall increased the rate of lizard cooling by conductively increasing heat loss to the burrow substrate. The importance of conductive heat loss was indicated by a comparison of cooling rates in burrows and in the freezer used to anesthetize summer field lizards. Even though $T_b - T_a$ values were up to three times greater in the freezer, cooling constants were considerably less (log a = -0.49 log body weight - 0.77, N = 5 lizards) than for animals of equal weight cooling in burrows. Freezer cooled iguanas sat on a 3 cm wide wooden strip that was at room temperature when the animal was strapped to it.

The slope of the $\ln(T_b - T_{be})$ vs. t lines remained constant on only 7 of 29 monitoring days. A single slope decrease occurred on 21 days at a mean T_b of 34.4 C (SD = 2.37, range = 30.0-39.6). A slope increase occurred during only one night's cooling. Slope decreases were probably due to a change in lizard posture, probably an increase in adductive contact of the limbs with the trunk and tail. Except for this movement, lizards remained quiescent until the hour before emergence, judging from observations in the laboratory and outdoor pen.

Burrow depth, as measured from the ground surface to the roof of the burrow terminus, averaged 32 cm (N = 8, SD = 25, range = 19-91) for adult females and 69 cm (N = 12, SD = 43, range = 25-183) for adult males (Iverson 1979). The greater depth of male burrows may be due both to the larger size of males and their greater site fixity over time. Lizards preferentially dug burrows in windblown, well drained sand along the sides of limestone ridges and at the edge of clumps of vegetation,

where roots helped prevent collapse of the burrow mouth. Lizards probably retreated nearly or completely to the end of the burrows each evening (see Burrow Movement).

Both higher nocturnal temperature and greater temperature stability may be determinants of the rather large mean burrow depth in *Cyclura*. Diurnal burrow temperature stability is not important since lizards did not usually use burrows as heat sinks. With no surface vegetation and except during heavy rain, soil temperature over a 24 hour period in June varied less than 1 C at depths of 25 cm or more. Soil temperatures at depths of less than 25 cm exceeded the nearly stable, 25 cm depth temperature during the day and early night and fell below the 24 cm level as the next sunrise approached. This depth corresponds well with the average female burrow depth. An adult lizard chose a ground surface retreat on only one occasion during the study. He retreated into a pile of limestone rubble during a late afternoon overcast period, rather than walking the 40 m to his only sand burrow. T_{be} was 24.1 C, 4.1 C below the lowest T_{be} recorded in his sand burrow. T_b's at 0730 for Lizard 3, confined in a field cage in October, were 25.7, 26.0, and 28.0 C, all below T_{be} for the same free-ranging lizard ($\bar{X}$ = 29.6, range = 28.8-30.2, N = 9). Winter burrow temperature stability may be even more important in determining average burrow depth than summer stability. Lizards equilibrated with minimum surface temperatures during cold fronts would barely be able to crawl. Seasonal variation in mean T_{be} probably did not exceed 4 C.

Females laid their single clutch of eggs at the end of a burrow and plugged part of the length with sand, leaving the eggs in an isolated, air-filled chamber. The depth of the egg chamber was commonly less than

other parts of the burrow, providing easier vertical escape for the hatchlings (Iverson 1979) as well as higher mean incubation temperatures.

Even though *Cyclura* did not plug its burrow, except during nesting, relative humidity should be close to 100 percent at the terminus (McNab 1966), due to the average burrow's considerable length (male $\bar{X}$ = 4.39 m, female $\bar{X}$ = 3.09; Iverson 1979). This has obvious value in water conservation, especially during the dry season. Capillary rise in water from the fresh water lens under Pine and Water Cays may increase the percent saturation of the burrow soil in lower lying areas. Since it requires two inches of rainfall to raise very sandy soil to field capacity (water weight = 5 percent of soil dry weight) to a depth of two feet (Meyer and Anderson 1952), the average burrow would rarely be elevated to this level. However, soil saturation of only one percent was sufficient to raise relative humidity to nearly 100 percent in pocket gopher burrows (Kennerly 1964).

T_{be}'s varied slightly for the same lizard when using different burrows. For example, Lizard 8 had mean T_{be}'s of 28.7 (N = 3) and 31.1 (N = 2) for two of its three sand burrows, presumably of different depths. Different lizards sometimes had slightly different mean T_{be}'s (Table 14). The greatest mean difference was 2.3 C (maximum difference = 3.2 C), between Lizard 12 in August and Lizard 13 in September. Comparisons between juveniles and adults would probably prove more striking. The samples were too small to determine whether burrow temperature influenced operant T_b during the day.

Table 14. Lizard body temperature at emergence in the field.

MONTH	LIZARD	SITE	NUMBER OF BURROWS UTILIZED	N (DAYS)	$\bar{X}$ T_{BE}	SD	LOW	HIGH	RANGE
Feb	1	II	1	4	26.3	1.2	24.5	27.0	2.5
Feb	2	II	1	7	25.7	0.6	25.0	26.9	1.9
Feb	3	II	2	2	-	-	25.2	27.8	2.6
				13	26.1	1.0	24.5	27.8	3.3
June	8	I	3	7	29.5	1.2	28.6	31.8	3.2
June	9	I	2	8	29.5	0.1	29.4	29.5	0.1
July	10	II	2	9	30.1	0.8	28.2	31.0	2.8
July	11	II	1	15	28.1	0.2	27.7	28.5	0.8
				39	29.1	1.0	27.7	31.8	4.1
Aug	12	I	2	3	30.1	-	29.2	30.2	1.0
Sept	13	III	2	5	27.8	1.0	26.8	28.8	2.0
				8	28.6	1.3	26.8	30.2	3.4
Oct	2	II	2	4	27.7	-	24.1	29.5	5.4
Oct	3	II	2	9	29.5	0.3	28.8	30.0	1.8
				13	29.0	1.5	24.1	30.0	5.9

ETHOLOGICAL ASPECTS OF THE THERMAL BIOLOGY OF *CYCLURA CARINATA*

Lizard Activity

Burrow Movement

The results of monitoring Lizard 2 as it moved in its burrow are illustrated in Figure 32. Movements toward the burrow mouth prior to emergence occurred incrementally in up to four steps. The maximum pre-emergence activity time was probably greater than the 37 minutes recorded. When scared into its burrow, the lizard retreated a mean distance of only 1.25 m or 27 percent of the October burrow length. The lizard crawled far into the burrow in a single movement at the end of the day, sometimes advancing a short distance further later in the night. However, the animal went to the end of the burrow on only four of fifteen final submergences.

Control of Lizard Emergence and Submergence

Mean emergence and submergence times conformed to the seasonal change in photoperiod (Figure 33). Submergence times at the three different field sites were more irregularly related to sunset than emergence times were to sunrise. Submergence did not occur any earlier in relation to sunset in the dry months of February and March than in the wet months of October and December, even though the latter months were slightly warmer. Apparently, activity times were not reduced due to lack of water during the dry season. Mean activity time decreased

Figure 32. Lizard movements in a burrow. Six days of monitoring in October and six in February are represented for Lizard 2 in a single, unbifurcate sand burrow, 4.6 m long in October and 3.9 m long in February (horizontal dashed lines). The October record was seven days long, with a one day gap on the fourth day. Dotted lines mark lizard movements in the burrow when I was not present. The lizard was periodically scared into its burrow (triangles). The letter E indicates emergence.

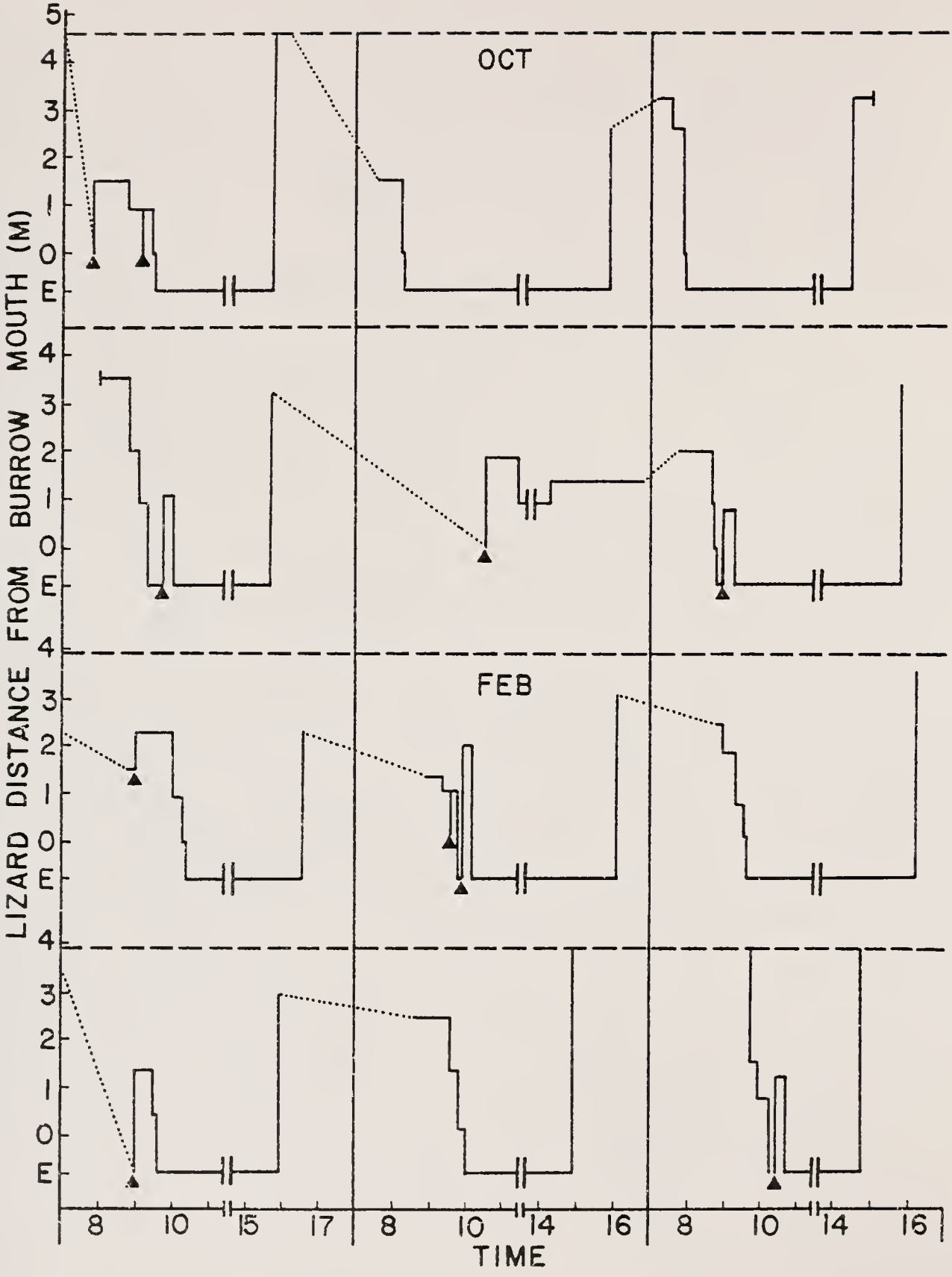
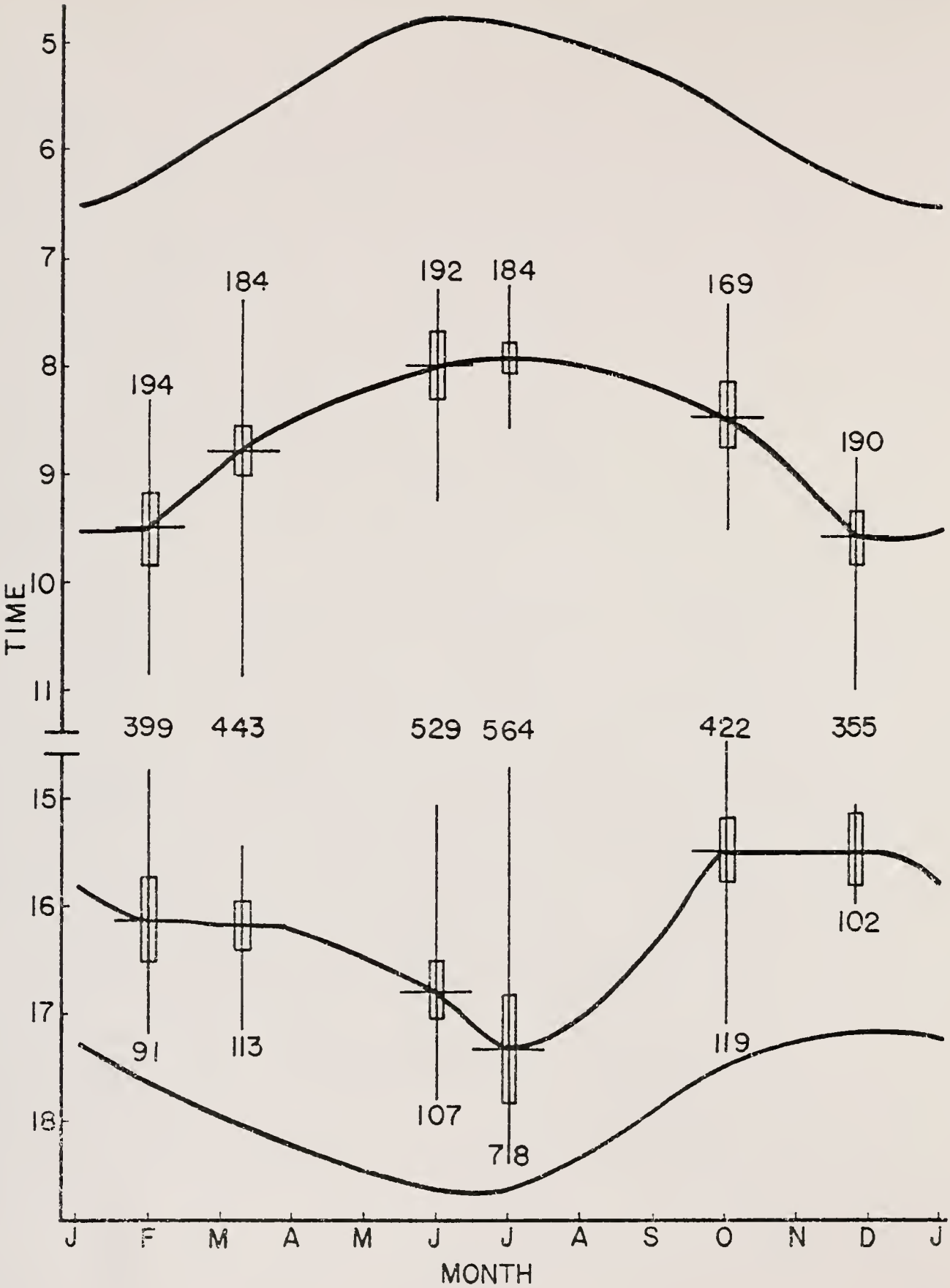

OCT
FEB
LIZARD DISTANCE FROM BURROW MOUTH (M)
TIME
8
10
15
17
8
10
14
16
8
10
14
16
E
0
1
2
3
4
5

Figure 33. Seasonal change in lizard emergence and submergence times. The upper and lower curves indicate the times of sunrise and sunset, respectively. Emergence and submergence times lie within. Vertical lines are ranges, horizontal lines are means, and rectangles are plus and minus two standard errors of the mean. The three sets of numbers refer to the minutes between sunrise and mean emergence time, mean emergence and submergence times or the mean activity time, and mean submergence time and sunset. February, July, and October data were collected at Site II, June data at Site I on Water Cay, and March-April, November-December data were collected on Pine Cay (Iverson 1977).


5
6
7
8
9
10
11
TIME
194
184
192
184
169
190
399
443
529
564
422
355
15
16
17
18
91
113
107
718
119
102
J
F
M
A
M
J
J
A
S
O
N
D
J
MONTH

three hours and 26 minutes or 37 percent between July and December. The earliest observed emergence occurred almost two hours after sunrise, at 0640 on Pine Cay in July (Iverson 1979). The latest observed submergence was by Lizard 11 at 1825 on Water Cay in July, 15 minutes before sunset and 35 minutes after the sun was no longer visible to the lizard.

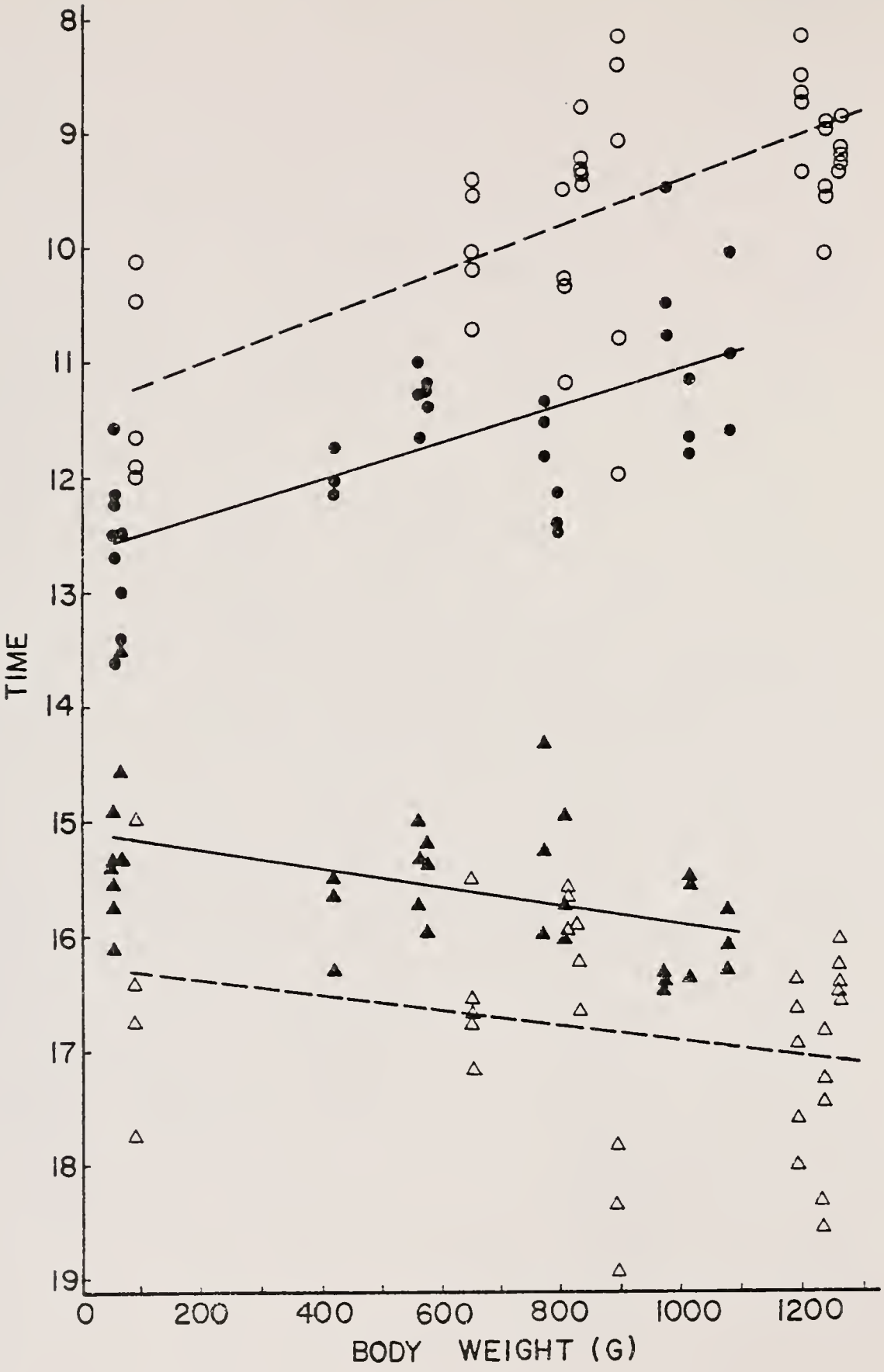
Emergence and submergence times varied with the illumination times of early morning and late afternoon basking sites, in turn influenced by variations in relief and vegetational cover. Lizard 3's morning basking site was located on top of a north-south oriented limestone ridge adjacent to the Pine-Water Cay inlet. His late afternoon basking site was about three meters away on the same ridge, on the western side near the top, facing the late afternoon sun and protected from easterly winds. The basking sites of Lizard 2, another large male of similar body weight occupying an overlapping home range further inland, came into direct sunlight later and went into the shade earlier due to the lower elevation and obstructing vegetation. As a result, Lizard 3's mean activity times were 127 and 58 minutes longer than Lizard 2's in February and October, respectively. Lizard 3 should be a healthier animal due to having more time at regulating phase T_b's to digest its food. Lizard 3 was indeed more robust (43.2 and 47.7 g/cm snout vent length for Lizard 2, 53.9 and 57.3 g/cm SVL for Lizard 3 in October, 1975, and February, 1976, respectively). However, Lizard 2 increased in weight by 158 g between October and February, whereas Lizard 3 gained only 103 g. The home ranges of the two lizards were approximately equal in size, but the relative food abundance in the ranges were not determined. Relative fitness is best expressed as a reproductive output.

The females sharing the home ranges of Lizards 2 and 3 in February weighed 710 and 1135 g (Lizard 1), respectively. Lizard 1 was the largest female captured on either Pine or Water Cays and, thus, probably laid more eggs per clutch than Lizard 2's female. Although these comparisons are suggestive, a large sample of lizard pairs would have to be analyzed to determine whether significant differences in activity times influence individual fitness.

Sex related differences in emergence times did not occur but the data were contradictory. Lizard 8, an adult female at Site I in June, emerged earlier than Lizard 9, a dominant male. However, Lizard 1, an adult female at Site II in February, emerged later than Lizard 3, a dominant male. Lizards 1 and 3 often used the same burrow in February. Since Lizard 3 was the larger animal and always submerged last into their unbifurcate burrow, the order of emergence may have been predetermined. Dominant males were usually the last to submerge due in part to their low cooling rates caused by large body size. Also, dominant males had territorial priority over smaller males at the best late afternoon basking platforms.

Emergence and submergence times in the Gainesville pen depended on lizard size (Figure 34). The adult females and the lowest ranking subadult male emerged later and submerged earlier than the rest of the adult males. Adult females were subdominant to adult males except during the nesting season and except to the male at the bottom of the male linear dominance hierarchy, which every lizard chased. Correlation coefficients for the linear regression were -0.700 for summer emergence ($p \leq 0.0005$), -0.681 for winter emergence ($p \leq 0.0005$), 0.256 for summer submergence ($p > 0.05$) and 0.463 for winter submergence ($p \leq 0.005$).

Figure 34. Correlations of times of emergence and submergence with body weight in penned Gainesville lizards. July-August emergence and submergence times for eight lizards monitored for six days are represented by open circles and triangles and the dashed regression lines; December-February times for eleven lizards monitored for three days are represented by solid circles and triangles and the solid regression lines.


8
9
10
11
12
13
14
15
16
17
18
19
TIME
0
200
400
600
800
1000
1200
BODY WEIGHT (G)

Note the lower submergence r values. From the regression equations, a 50 g hatchling was active for 299 minutes in summer and 154 minutes in winter, 62 and 48 percent of the times for a 1200 g male. The summer and winter ranges for activity times in the pen were similar to the seasonal range of mean adult activity time in the field. It should be pointed out that lizard density in the pen was up to 134 times the 31.1 adults per hectare reported by Iverson (1979) for his Rocky Coppice field site.

Body temperature commonly declined slightly while a lizard paused near its burrow mouth prior to emergence or just after emergence prior to reaching a sun exposed location (25 of 52 records, Figure 5). This was usually the lowest T_b in the 24 hour period. The largest T_b drop recorded was 0.7 C for a male on Fort George Island in September. Usually, the decline was 0.3 C or less.

Body temperature at emergence ranged from 24.9 to 31.0 C in the field (Table 15). Temperature independent emergence was observed in the Gainesville pen in January at T_b's as low as 15 C, only 2.3 C above the critical thermal minimum. The minimum substrate temperature recorded on Pine Cay was 12.5 C (Iverson 1979). Thus, in a very shallow burrow or in rock rubble at the ground surface, T_b at emergence in the field may occasionally fall as low as 15.0 C.

Final submergence occurred at much higher T_b than emergence (Table 15). T_b's of only Lizards 4 and 11 in summer consistently fell below their regulating phase mean minima prior to submergence, to as low as 31.2 C for Lizard 4 during a fifteen minute rain and 34.3 C for Lizard 11 during late afternoon basking. Iverson (1977) also occasionally observed an adult *Cyclura* emergent during a heavy rain, presumably

Table 15. Emergence and submergence times, temperatures, and light intensities for free-ranging lizards in the field.

	EMERGENCE					SUBMERGENCE				
MONTH	N (DAYS)	$\bar{X}$	RANGE	SD	2SE	N (DAYS)	$\bar{X}$	RANGE	SD	2SE
				TIME OF DAY						
Feb	16	0931	0820-1053	39	20	16	1609	1444-1711	47	24
July	23	0756	0716-0835	19	8	19	1720	1445-1825	67	31
Oct	16	0829	0726-0930	36	18	16	1531	1431-1706	39	20
				BODY TEMPERATURE						
Feb	12	26.0	24.9-27.2	0.9	0.5	16	38.3	36.3-41.4	1.4	0.7
July	23	28.9	27.7-31.0	1.1	0.5	18	37.6	34.3-42.5	2.5	1.2
Oct	15	28.9	24.1-30.0	1.6	0.8	14	38.7	35.3-41.0	1.5	0.8
				LIGHT INTENSITY (FT-C)						
Feb	16	829	477-1298	243	122	15	509	251-972	198	102
July	24	680	390-1069	178	73	19	241	50-900	266	122
Oct	16	810	200-1400	282	141	16	309	88-700	138	69
				BLACK BODY TEMPERATURE						
Feb	16	44.6	36.4-50.5	4.5	2.2	15	37.3	30.4-46.1	3.6	1.9
July	24	41.7	32.0-50.0	4.6	1.9	19	39.0	28.6-49.4	5.2	2.4
Oct	16	43.5	33.6-51.7	4.5	2.2	14	38.5	33.4-43.6	2.6	1.4
				SUN EXPOSED SAND TEMPERATURE						
Feb	16	36.2	28.8-43.8	4.0	2.0	15	33.3	26.8-39.9	3.2	1.7
July	24	30.4	26.6-42.4	3.3	1.3	19	32.6	27.8-41.9	4.4	2.0
Oct	16	31.4	27.4-37.7	3.6	1.8	16	33.5	30.0-39.9	2.4	1.2

sometimes with T_b near burrow temperature. Adult lizards would have to remain emergent after sunset during clear weather for T_b to drop to near burrow temperature. This was never observed. Neither heat lamps suspended above the ground nor a plywood box with a metal lid heated from inside with incandescent lamps could induce *Cyclura* to remain emergent after sunset in the Gainesville pen. That is, submergence could be induced prematurely by foul weather but could not be extended into darkness even when sufficient heat sources were provided to permit T_b to remain in the regulating phase range.

Both light intensity and black body temperature were usually high at emergence (Table 15), significantly higher than at submergence ($p \leq 0.05$). Thus, *Cyclura* usually emerged only when its T_b would rapidly increase above burrow temperature. For example, Lizard 3 reached 29.6 C, the mean emergence T_b while free-ranging, at 0752, 0804, and 0817 while confined in a sun exposed field cage. The range of emergence times while free-ranging, 0727-0839, bracketed these cage times. Medium to heavy overcast during the normal emergence time of free-ranging iguanas, constituting 16 lizard days of the study, always delayed the emergence time. On two occasions in October, when the overcast lasted all day, none of the four monitored iguanas emerged. On five occasions, emergence was delayed until after the overcast cleared. On five other occasions, emergence was delayed yet occurred during overcast. T_b rose appreciably after emergence even though the sky was overcast. On only two occasions, both during the summer, did a delayed emergence occur which was not followed by an appreciable T_b rise. In one case T_b rose from 29.5 C to only 30.3 C in one hour and 59 minutes before the sky

cleared and T_b rose rapidly. In the other case, T_b declined from 30.2 C at emergence to 26.8 C before slowly increasing to 30.9 C, three hours and 42 minutes after emergence, when the sky cleared.

An iguana sleeping a meter or more below the ground near the end of a four meter long nonlinear burrow probably receives neither light nor temperature cues revealing the beginning of a new day. Morning arousal may be due to an internal biochemical timing mechanism or biological clock. A phase shift (phase delay) of clock timing was observed after release of all the summer lizards (Figure 35). Re-entrainment to the normal emergence time required three or more days. Submergence times were not affected. Lizards monitored during the three subsequent field trips did not exhibit delayed emergence. Thus, the delays must have been triggered by the bacterial infection following the summer implantation operation or, more likely, by some procedural step during the operation; for instance, cooling the lizards or keeping them awake during part of a normal sleep period.

After the biological clock initially gets the animal moving, a second emergence stimulus probably times the final emergence stage starting near the burrow mouth. High light intensity, one possible second stimulus in this two step stimulus-response chain, results in initiation of the final emergence stage. On the other hand, low light intensity due to heavy overcast inhibits emergence. The final emergence stage commonly required two steps. First, the lizard extended its head above the ground surface. This usually required exposure of most of the trunk, since in sandy soils the burrow mouth was in the side of a cone shaped depression. After a pause, the lizard quickly walked to

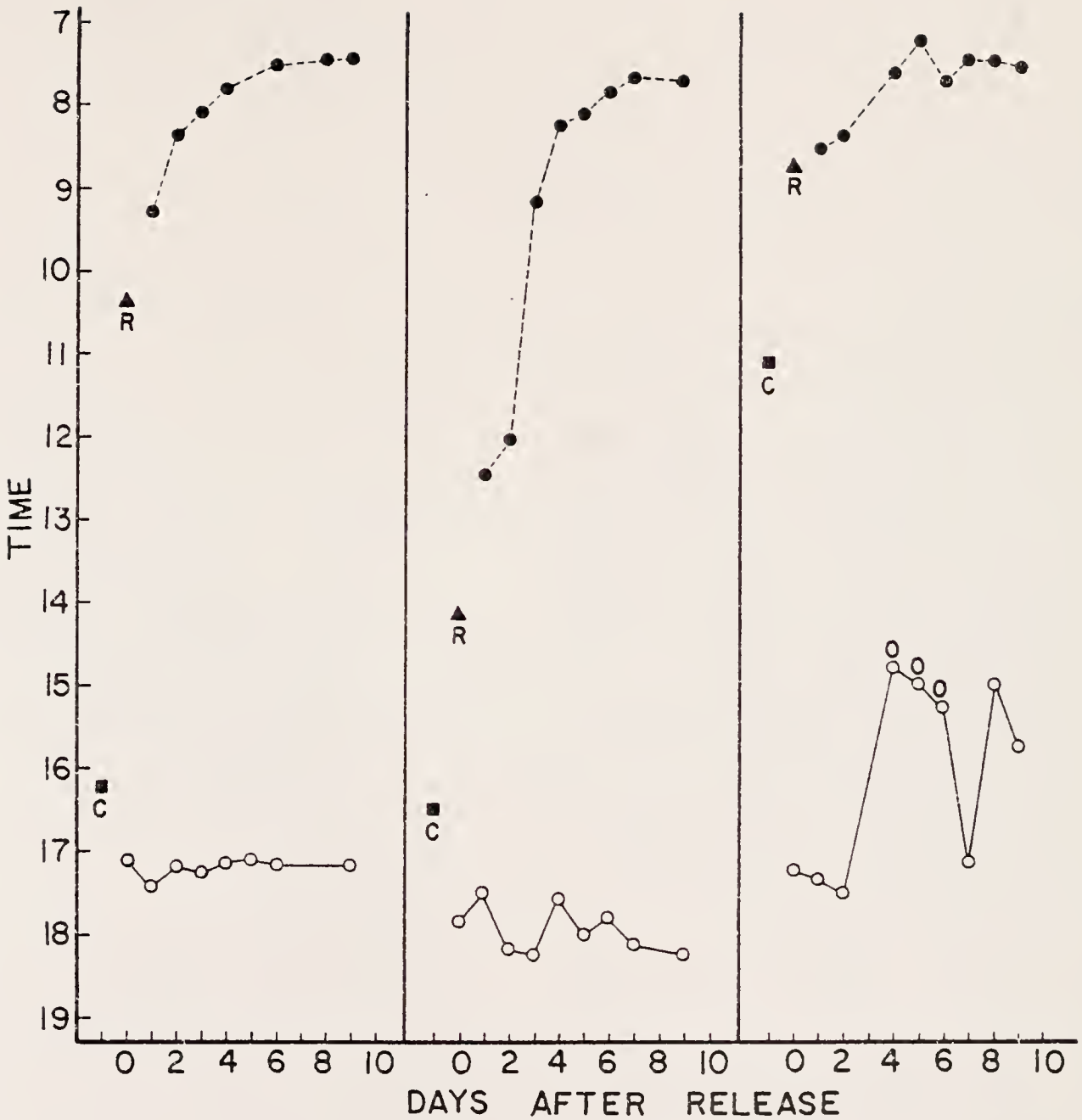


Figure 35. Gradual reentrainment of lizard emergence times after release. Emergence times (dashed lines) and submergence times (solid lines) of Lizards 9 (June), 11 (July), and 10 (July) are displayed from left to right. Capture time, release times, and overcast skies are indicated by the letters C, R, and O, respectively.

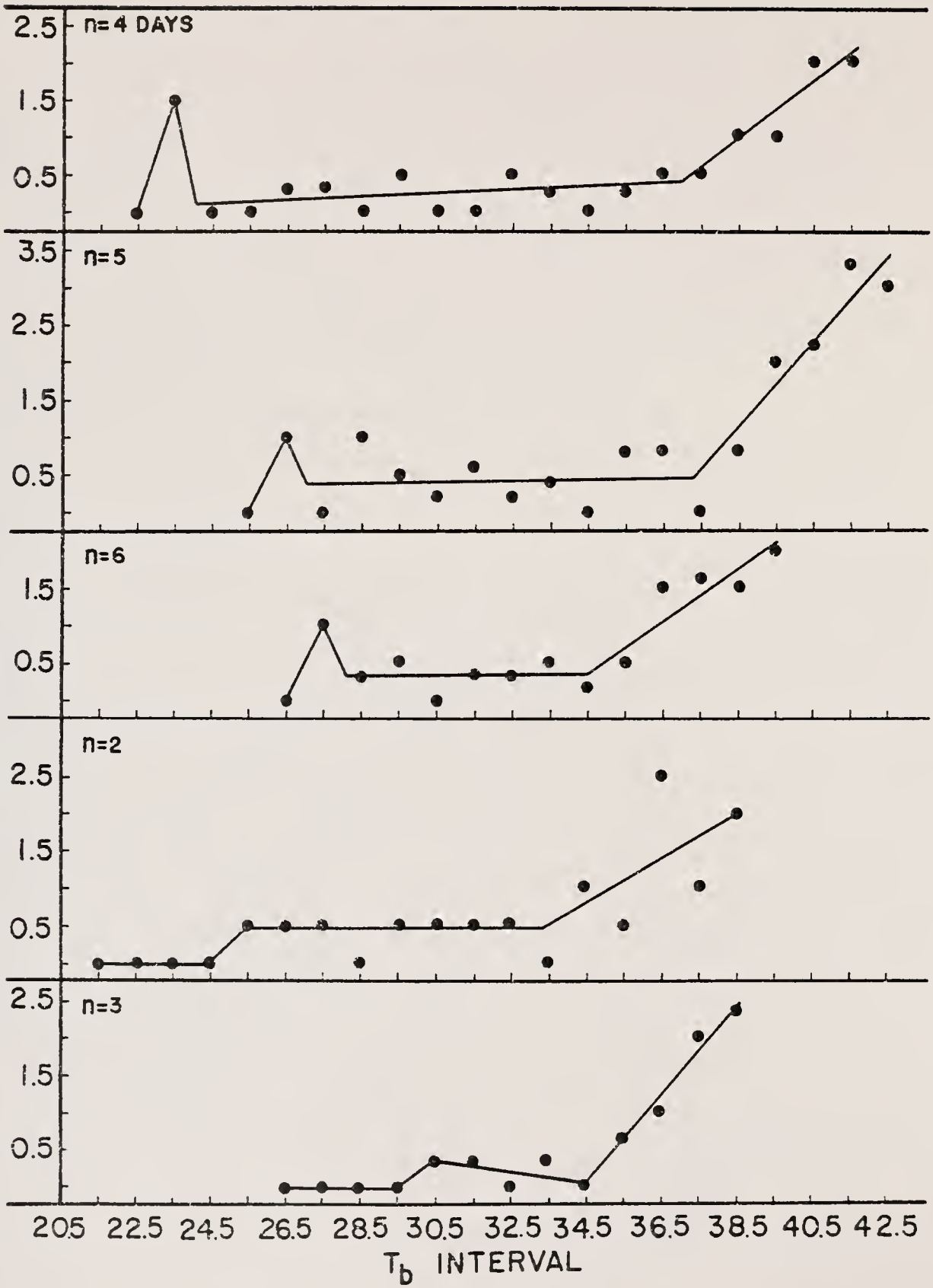
level ground. Due to the surrounding vegetation, lizards were still commonly in the shade. For example, Lizard 11 had to walk four meters to reach its morning basking site. Thus, *Cyclura* did not consistently heat its head prior to complete emergence. Lizards were much more likely to retreat into their burrows when scared after a recent emergence. This inverse relationship between shyness and T_b, first reported for *Anolis lineatopus* (Rand 1964), is probably a common characteristic of diurnal lizards.

Since the Gainesville pen in July received only 48 percent as many minutes of direct sunlight during clear weather as Site II, lizard activity periods were expected to be commensurately reduced. However, large males and an occasional adult female emerged and submerged when the pen was totally in the shade. As a result, the mean activity time of seven adults was 468 minutes or only 17 percent less than the 564 minute mean for two males at Site II. It appears that *Cyclura* has an innate minimum daily activity period as well as a maximum activity period. When the time T_b can be maintained within the preferred range is reduced below the minimum activity period, the lizard operates at a lower mean T_b rather than remaining in its burrow.

Morning Heating Phase

The typical movement pattern during emergence, basking, and the initial minutes of the first foray is illustrated in Figure 36. The initial blip on the upper three records corresponds to the short walk in the Gainesville pen from the burrow mouth to the morning basking site. Morning and late afternoon basking in the field each occurred at only one or at most two locations, different for morning vs. afternoon

Figure 36. Lizard activity during the morning heating phase. Results are displayed for five adult lizards confined either in the Gainesville pen or in a field cage (bottom two graphs). Except for brief intervals at high T_b's, lizards were continually in direct sunlight. A movement unit was defined as any change in lizard location; that is, a cage climbing bout, a feeding bout, a reorientation to the sun, or a short walk. Two regression lines were fitted to the data, each covering a segment of the T_b range.


n=4 DAYS
n=5
n=6
n=2
n=3
2.5
1.5
0.5
3.5
MEAN MOVEMENT UNITS / 1° C
20.5 22.5 24.5 26.5 28.5 30.5 32.5 34.5 36.5 38.5 40.5 42.5
T_b INTERVAL

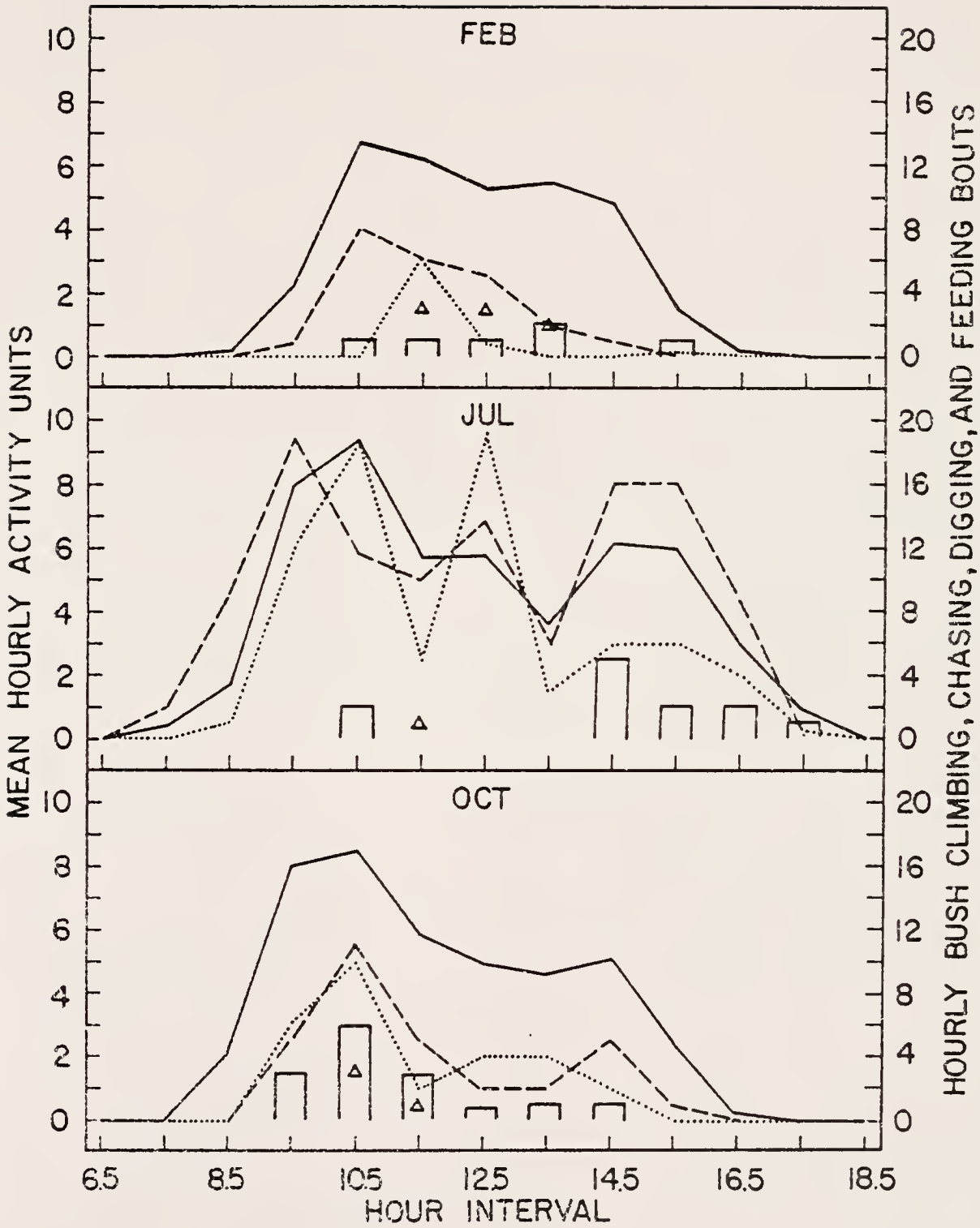
basking and always located quite near the present home burrow. Lizards which emerged in the shaded Gainesville pen moved from filtered sun spot to sun spot without increasing their T_b significantly, resulting in higher initial activity peaks than for the lizards illustrated in Figure 36. Lizards settled down after arrival at a sunlit location to a low, essentially temperature independent rate of movement. Animals occasionally fed or engaged in social interactions for short periods during this interval, as well as displaying intermittent thermoregulatory behavior. Strenuous activity was sometimes elicited in the basking iguana, as when an adult male on his first foray encroached into the area and was chased away. Activity abruptly increased between T_b's of 34 and 37 C, corresponding to the start of the first foray.

The duration of the morning heating phase for similarly sized adult males did not differ significantly from February to October. Pooled data had a mean of 104 minutes, a range of 57-166, and a SD of 30 (N = 46 clear days). Lizards in winter sometimes basked up to 300 minutes without even completing the heating phase or starting a foray (Iverson 1977, November 27-December 21 field trip).

Regulating Phase

Maximum daily activity from February to October occurred during the first foray (Figure 37). The same timing was observed in the pen, where lizard movement could be quantified more precisely. Activity decreased to a minimum in the early summer afternoons due to the high surface temperatures over most areas. Bimodality nearly disappeared during the cooler months of February and October and, as observed by Iverson (1979), disappeared in November and December. Dominant males

Figure 37. Daily and seasonal variation in activity. Lizards were observed for 15 days in each of three months at Site II. A walking bout (solid line) observed from the blind (July) or during tracking (February and October), digging out a burrow (open triangles), climbing a bush (histograms), chasing another lizard (dotted lines), and feeding (dashed lines) on sardines (July only), fruits, or leaves were all counted as one activity unit and the units summed for the 15 day periods. Total mean hourly activity units are represented by solid lines. Observations in hours with more than ten minutes of overcast were not included. Separate months should not be compared quantitatively since lizards declined in numbers between trips, supplemental food was provided in July, and lizards were observed from a blind in July, tracked in October and February.


FEB
JUL
OCT
MEAN HOURLY ACTIVITY UNITS
HOURLY BUSH CLIMBING, CHASING, DIGGING, AND FEEDING BOUTS
HOUR INTERVAL
6.5
8.5
10.5
12.5
14.5
16.5
18.5
0
2
4
6
8
10
12
16
20

were territorial all year, defending an area around their home burrow primarily by chasing intruding dominant males and smaller subdominant males away. The three July chase peaks occurred during the first to the third forays of the dominant male, when the probability of his making visual contact with another lizard on a foray was greatest. Similarly, the two chase peaks in October occurred during the first foray and the second or third forays, respectively, and the single February chase peak occurred while lizards were on their first or second forays. The loss of the second and third maxima in February was due to a decrease in the length of the activity periods as well as declines in territorial behavior and the number of subdominant males from five to three. The daily variation in the number of feeding bouts corresponded well to the number of chases, declining from three peaks in July to two in October and one in February. Maximum feeding activity in July occurred before the mean activity and chase maxima, due to lizards walking en masse to the sardines immediately after morning basking. Wild Dilly fruit (*Manilkara bahamensis*) profusely scattered on the ground produced a similar response in February.

Arboreal activity was observed much more frequently at Iverson's Pine Cay site, probably due to a number of differences at Site II; that is, lower lizard density (an estimated maximum of 13.4 vs. 31.1 adults per hectare), greater average size of adults, lower density of food species, disturbance of lizards due to tracking, and, perhaps, higher wind speed. Arboreal activity crudely mirrored chases and feeding (Figure 37). The absence of climbing during July mornings may be due to the supplemental sardine feeding. Iverson (1977) observed maximum

arboreal activity without concurrent feeding at midday in June to September and during the morning in November and December. The former may have been an escape behavior from hot surface microclimates and the latter a seeking of warmer basking platforms. The mean change in T_b was +0.4 C (range = -0.6 to +2.0, SD = 0.8) for 11 bouts of adult arboreal feeding in October at Site II ($\bar{X}$ time/bout = 7.5 min, range = 1-23, SD = 7.0).

Lizards were occasionally observed digging out their burrows in the field and the pen. Excavation almost always occurred between 1000 and 1400 during the first or second forays. The currently occupied burrow was more commonly excavated than those presently unoccupied or used by other lizards. An excavation by Lizard 2 in February lasted from 1128 to 1225 and resulted in a T_b drop from 37.2 to 35.4 C. Another bout in October by Lizard 14 lasted from 1055 to 1114 and resulted in an overall T_b rise from 39.6 to 39.8 C. In each case the lizard disappeared into the burrow for up to six minutes, periodically kicking sand up to three meters out the mouth, emerging and basking briefly, then reentering the burrow for more digging. Six submergences occurred during both the February and October observations, averaging 3.3 and 1.2 minutes per submergence, respectively. Immediately after laying her eggs in the cage burrow, Lizard 6 performed the same digging behavior in the reverse direction, plugging the egg chamber with sand scraped and kicked into the burrow from the area immediately outside the mouth. The sand for burrow plugging may normally be obtained entirely from inside the burrow. This was impossible in the cage due to insufficient sand. Nest plugging began at 0930 and ended at 1339 after 29 emergences. T_b ranged from 36.6 to 39.4 C. Since nesting

apparently occurs before morning emergence in free-ranging females (Iverson 1977), T_b may not normally rise much above burrow temperature.

Heavy cloud cover inhibited lizard activity. The daily activity unit sum was negatively correlated with the percent daily overcast time ($Y = -0.67\ S + 57.9$, $r = -0.697$, $N = 15$ July days, $p \leq 0.005$). The effectiveness of cloud cover as an activity inhibitor varied with its timing during the emergent lizard's day (Figure 38). The first peak in inhibitory effectiveness occurred during the hour before maximum hourly activity, when most lizards were just starting their first forays. Cloud cover was less effective as an activity inhibitor during the normal peak activity period. Maximum inhibition occurred in midafternoon. Practically any short period of heavy overcast during this period delayed and reduced the 1400-1600 activity peak. Lizards which retreated into their burrow during heavy midafternoon overcast usually did not reemerge until the next day, even when the skies cleared before the normal submergence time.

Foray Movement and Body Temperature

After basking for a time near the home burrow following emergence, iguanas rather abruptly started the first of two to four daily forays ($\bar{X} = 2.4$ for February plus October). Lizards walked for a few meters at a fairly constant rate, usually moving in nearly a straight line, frequently licking rocks, organic debris, and potential food items between strides, then pausing for a short time in either an exposed or shaded location before walking another few meters. Change in the direction of travel usually occurred after a pause rather than during a walk. Lizards paused and tilted their heads sideways upon arrival at

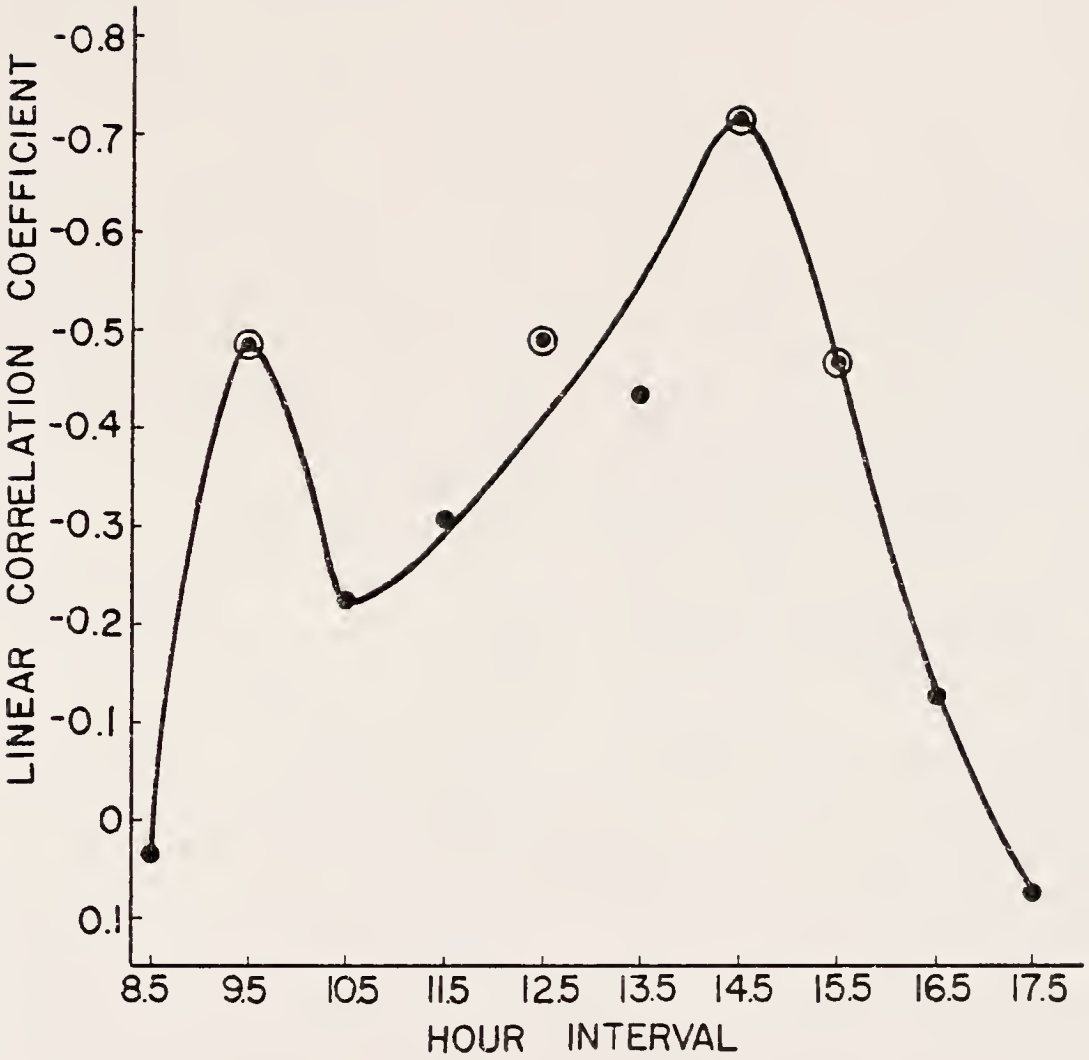


Figure 38. Variable inhibitory effectiveness of cloud cover on lizard activity. Regression coefficients were calculated for hourly linear correlations of percent cloud cover vs. total lizard activity units. The sample consisted of fifteen days of observations at Site II in July. Significant correlations at the five percent level or higher are circled. The curve was fitted by eye.

an arboreal food source, then commonly climbed the bush. A search pattern restricted to the immediate area was initiated when a preferred fruit was found on the ground. Forays were circular, elliptical, or linear, usually starting and ending at the burrow utilized the previous night. Chases and other social interaction occurred after initial visual contact, when two lizards met during their forays or when one lizard was on a foray and another was resting near its home burrow during an interforay (see Iverson 1979 for details of *Cyclura carinata* social behavior).

Mean distances traveled during forays and mean rates of travel were greater in February than October. Since the differences were not significant, the two months of data were pooled. The greater abundance of fruit in October may have resulted in the slightly smaller home ranges and slightly lesser distances traveled. The mean distances traveled during first, second, and third forays on clear or nearly clear days were not significantly different: means = 132.9 m (436 ft), 145.1 (476), and 121.9 (400); 2 SE = 21.3 (70), 15.2 (50, and 33.2 (109), respectively. The mean rate of travel declined from first to third forays, but not significantly: means = 1.41 m/min (4.63 ft./min), 1.24 (4.08), and 1.15 (3.77), 2 SE = 0.30 (0.97), 0.19 (0.63), and 0.61 (1.99) respectively. With the sun obscured by clouds 0-20 percent of the time, the overall mean rate of travel was 1.25 (4.10) [N = 32, SD = 0.51 (1.68), range = 0.36-2.54 (1.77-8.33)]. *Iguana iguana* weighing slightly less than the *Cyclura carinata* tracked in the present study could walk at a maximum rate of approximately 3.4 m/min (T_b = 30 C) and 4.0 m/min (T_b = 38 C, 1.8 C above mean operant T_b) without incurring a significant oxygen debt (Moberly 1968). Thus,

walking in *Cyclura* was probably an aerobic activity, with little or no build-up of lactic acid, leaving a margin of safety for more strenuous activities; such as, bush climbing, chasing, burrow digging, and infreqently, fighting.

Foray length was not depressed until overcast time reached 45 percent or more of total foray time (Figure 39). High surface temperatures during perfectly clear days also depressed the maximum foray distance attained. This effect was probably greater during the summer. The mean rate of travel was inversely correlated with overcast time. Lizards moved to a warm exposed substrate and sat quietly in a prostrate posture during overcast. Since this nonwalking time increased as cloud cover time increased, the rate of travel decreased.

Both foray length and the mean rate of travel were independent of mean body temperature between 35.0 and 40.5 C (Figure 40). However, no foray occurred outside this mean T_b range. Also, when overcast time was 30 percent or less, mean T_b was inversely correlated with the mean rate of travel. Lizards had to spend more time sitting in the shade avoiding overheating when their mean T_b's exceeded the preferred range during clear and nearly clear days, thus decreasing the mean rate of travel.

Mean T_b was significantly lower at the start of the first foray than at the start of subsequent forays (Figure 41). Also, the mean T_b range during a foray declined from Foray I to III (February: I; $\bar{X}$ = 5.3 C, SD = 2.6, II; $\bar{X}$ = 1.6, SD = 0.8, III; $\bar{X}$ = 0.9, SD = 0.6. October: I; $\bar{X}$ = 4.0, SD = 2.5, II; $\bar{X}$ = 1.7, SD = 1.0, III; $\bar{X}$ = 1.5 C, SD = 1.2). Thus, lizards were more eurythermal during the first foray than during subsequent forays. Mean T_b at the start of the first foray

Figure 39. Influence of cloud cover on the length of lizard forays and the mean rate of travel during forays. Data for February and October tracking of large male *Cyclura* have been pooled (N = 6, $\bar{X}$ weight = 1711 g, range = 1507-1864). The mean rate of travel equaled the total distance walked during a foray divided by the total time required. Solid and dashed lines are linear regressions for 0-45 and 0-58 percent overcast times, respectively. Neither correlation in the upper graph was significant (solid line; r = -0.035, dashed line; r = -0.111, $p > 0.05$) while both correlations in the lower graph were significant (solid lines; r = -0.292, $p \leq 0.05$, dashed line; r = -0.494, $p \leq 0.0005$).

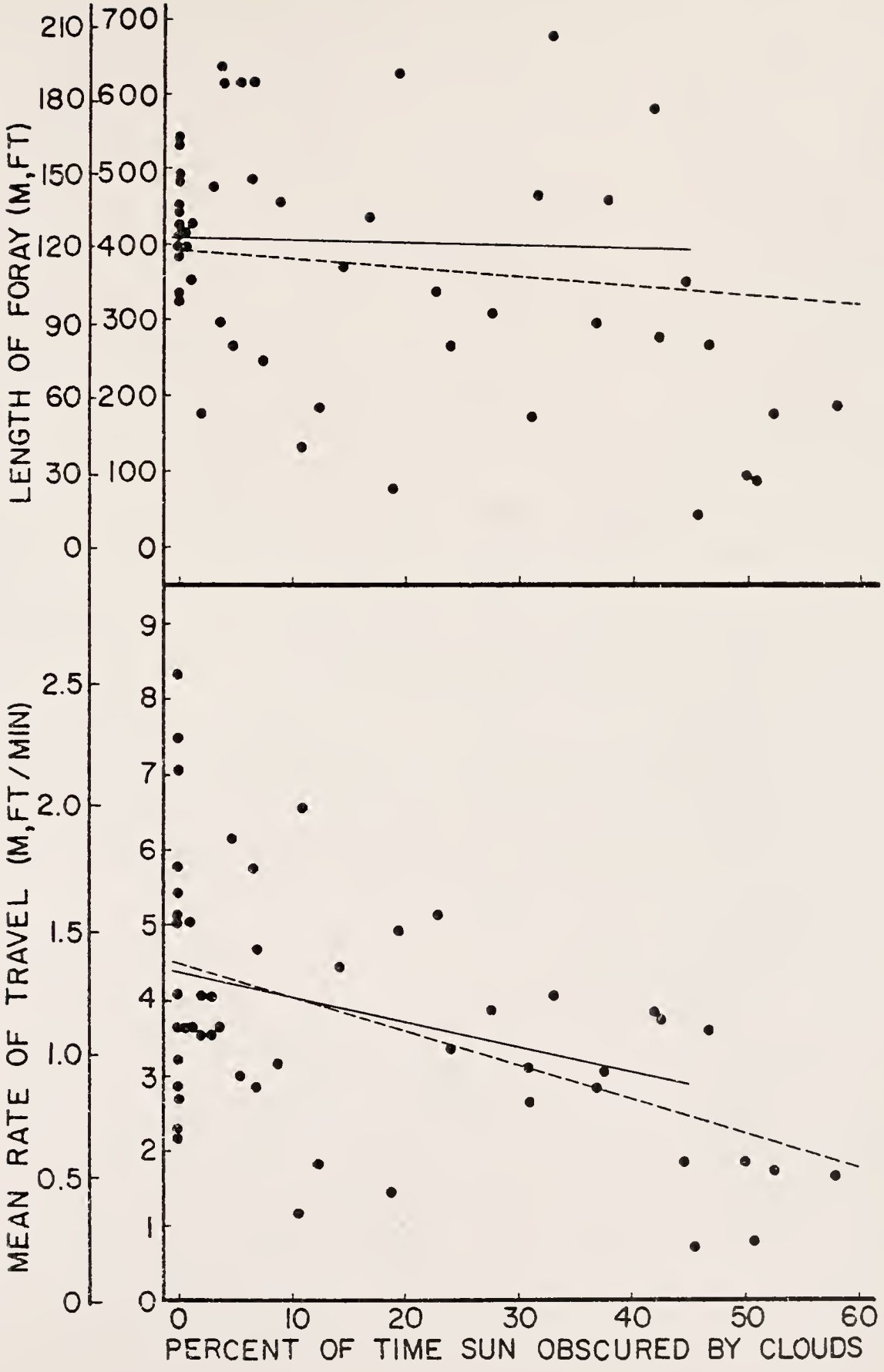

LENGTH OF FORAY (M,FT)
210
180
150
120
90
60
30
0
700
600
500
400
300
200
100
0
MEAN RATE OF TRAVEL (M,FT/MIN)
2.5
2.0
1.5
1.0
0.5
0
9
8
7
6
5
4
3
2
1
0
0
10
20
30
40
50
60
PERCENT OF TIME SUN OBSCURED BY CLOUDS

Figure 40. Correlations of foray length and rate of travel with mean body temperature. The percent overcast times are represented by solid circles (zero percent), open circles (1.0-9.1), open triangles (10.7-27.5), and open rectangles (31.2-58.0). Solid lines are linear regressions for all the data points (upper graph; $r = -0.032$, $p > 0.05$, lower graph; $r = -0.062$, $p > 0.05$). The dashed line is the regression for 0-30 percent overcast time ($r = -0.370$, $p \leq 0.01$).

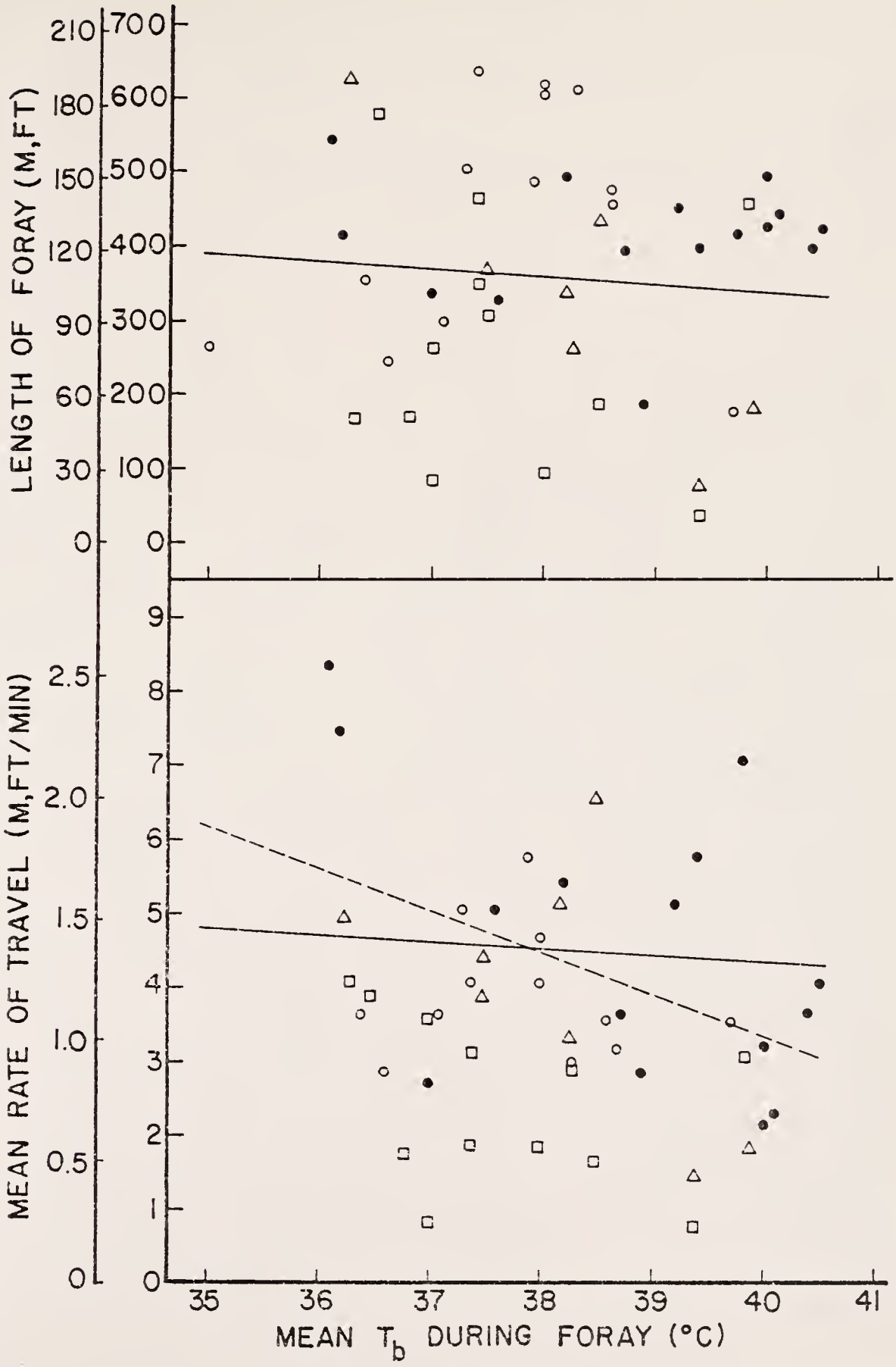
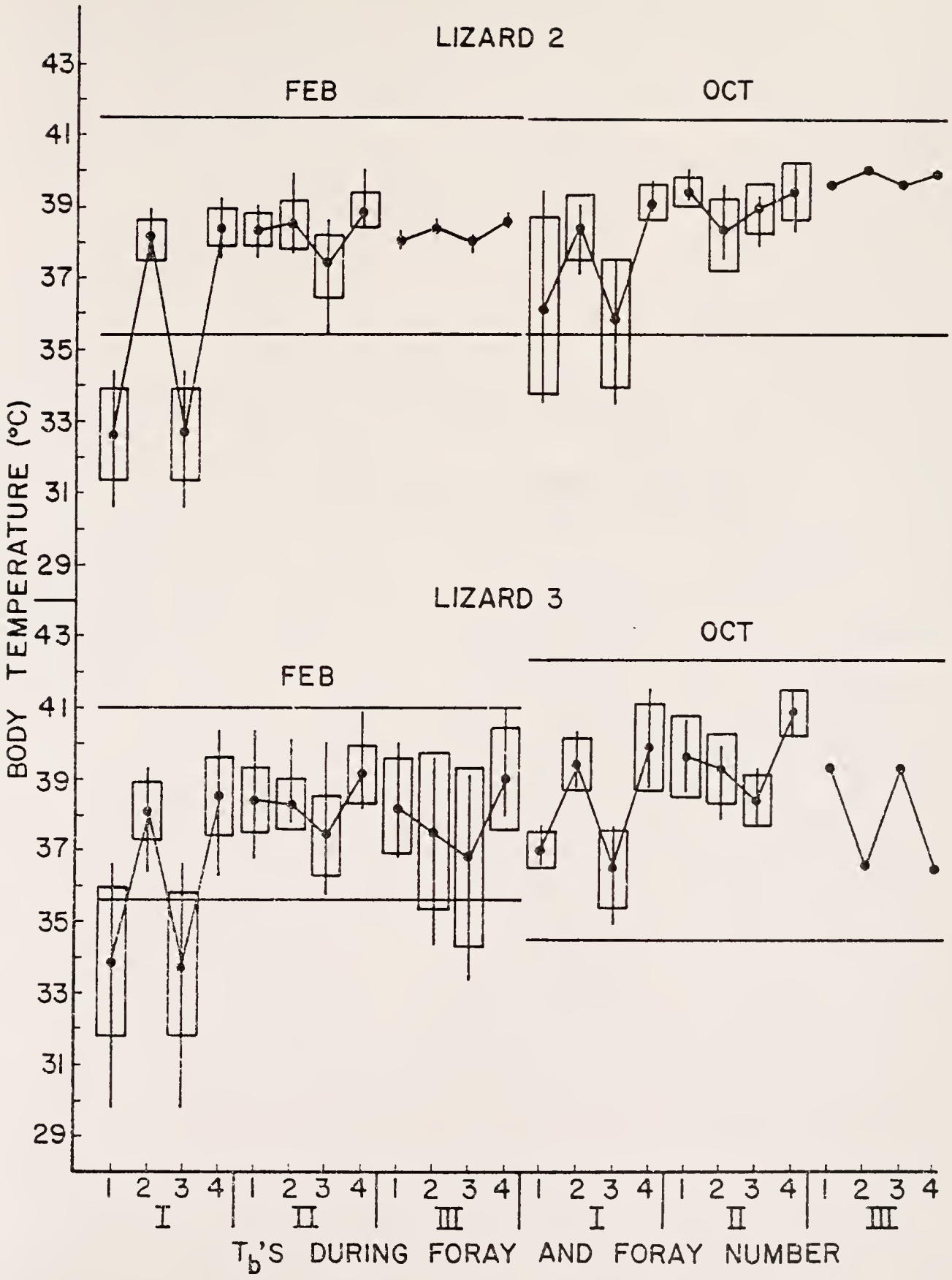

LENGTH OF FORAY (M,FT)
210
180
150
120
90
60
30
0
700
600
500
400
300
200
100
0
MEAN RATE OF TRAVEL (M,FT/MIN)
2.5
2.0
1.5
1.0
0.5
0
9
8
7
6
5
4
3
2
1
0
35
36
37
38
39
40
41
MEAN T_b DURING FORAY (°C)

Figure 41. Body temperatures during forays. Data are illustrated for two lizards monitored in both February and October. Arabic numbers below the abscissa refer to T_b's at the start (1) and end (2) of Forays I, II, and III and minimum (3) and maximum T_b's (4) during the forays. Diagonal lines connect mean T_b's, vertical lines are ranges, and rectangles are plus and minus two standard errors for $N \geq 4$ days. Horizontal lines are the lizard's minimum and maximum voluntary tolerances during the regulating phase.


LIZARD 2
FEB
OCT
LIZARD 3
FEB
OCT
BODY TEMPERATURE (°C)
43
41
39
37
35
33
31
29
1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4
I II III I II III
T_b'S DURING FORAY AND FORAY NUMBER

in February was usually even below the minimum voluntary tolerance of the regulating phase. Lizards may become more eurythermal during the first foray during the time of maximum seasonal activity. Iverson (1977) observed that *Cyclura* was most active in March and April, only one month after my February monitoring.

T_b usually both increased and decreased during a foray rather than steadily increased or decreased. The T_b at the start of the foray was lower than the maximum T_b during the foray in 91.4 percent of total forays and was higher than minimum T_b during the foray in 75 percent of second plus third forays. Except during the opening minutes of the first foray, T_b was usually near the middle of the regulating phase range. Thus, lizards had upper and lower thermal buffers to accommodate less frequent maximal T_b changes, for example, an unavoidable T_b rise during feeding atop a bush or an unavoidable T_b fall during a long overcast period.

No heating nor cooling trend was evident when T_b's at the start of interforays were compared to those at the start of the next foray. Thus, lizards didn't consistently return to the home burrow to heat or cool before the next foray. The interforay was probably important in reorienting the lizard in its home range prior to further walking.

Cyclura is apparently capable of some seasonal acclimatization of its metabolic rate. Activity in the thermal gradient, as measured by the number of shuttling movements and the daily distance walked, was greater in lizards acclimatized to winter than to summer weather in Gainesville (Table 16). The difference between samples was greatest during the second day in the gradient and had decreased considerably by the fourth day. Except for the second day, the magnitudes of the differences in shuttling movements were greater than in the distance walked.

Table 16. Possible acclimatization of lizard activity. Lizards were kept in outdoor pens in Gainesville, then monitored in the thermal gradient for four days. The two samples each consisted of two males and two females matched for approximately equal size and weight. Air temperature and photoperiod were held constant. The mean T_b's for the two samples did not differ significantly. A one-sided t test was used to test for differences in the number of daily shuttling movements and the daily distance walked.

	DAILY SHUTTLING MOVEMENTS						DAILY DISTANCE WALKED(M)					
	JULY		DEC-JAN				JULY		DEC-JAN			
DAY	$\bar{X}(1)$	SD	$\bar{X}(2)$	SD	$\frac{(1)}{(2)} \cdot 100$	P	$\bar{X}(1)$	SD	$\bar{X}(2)$	SD	$\frac{(1)}{(2)} \cdot 100$	P
1	5.5	3.3	11.5	14.8	47.8	NS	3.23	1.19	2.71	2.35	119.1	NS
2	9.5	5.4	27.8	15.2	34.2	0.05	3.29	1.52	11.06	6.83	29.8	0.05
3	19.8	6.8	39.5	26.1	50.1	NS	10.70	4.82	16.00	7.13	66.9	NS
4	27.8	8.6	34.7	4.1	80.1	NS	17.25	7.71	20.06	1.16	86.0	NS
1-4	15.6	10.6	28.4	18.7	54.9	0.025	8.63	7.35	12.47	8.20	69.2	NS

Feeding, Transmitter Passage Time, and Defecation

Lizards occasionally fed briefly on the ground near their home burrows before basking or starting their first forays. The mean T_b for feeding on the ground in February plus October was 36.7 C (N = 14, range = 30.0-40.4, SD = 2.42). However, arboreal feeding did not begin until the first foray, at a significantly higher mean T_b than ground feeding (N = 13, $\bar{X}$ = 38.6 C, range = 35.7-40.1, SD = 1.39, $p \leq 0.01$, one-sided t-test). Also, both the feeding rate and the amount of food consumed in the Gainesville pen were significantly less immediately after emergence (Table 17). The mean feeding rate was 50-52 percent less and the mean amount consumed was 38-43 percent less than during the regulating phase. Yet, one recently emerged lizard consumed white grapes equivalent to 8.4 percent of its body weight. Clearly, the T_b range for feeding was quite broad, approximately 23.6 C to probably greater than 40.4 C. One advantage of low T_b feeding is the capacity to quickly exploit new food sources on the ground near the home burrow; for example, fruits which fall during the night, before other lizards already on their first forays discover the source.

The time required for passage of transmitters through the digestive tract varied from 2.8 days for a far-field transmitter in a free-ranging lizard in October to 66 days (2 Jan-8 Mar) for a near-field transmitter in a lizard in the Gainesville pen. Passage times increased during the Gainesville winter, probably due to both the cessation of feeding and low T_b's. Passage times for free-ranging lizards at Site II in October varied considerably (2.8, 4.8, 7.0, and 11.0 days for far-field transmitters; more than 13 days for a near-field transmitter). Although

Table 17. Effect of body temperature on the feeding rate and meal size of penned *Cyclura carinata*. Lizards were provided with white grapes ad libitum as a food source. Data were collected in July and August in Gainesville.

TIME OF FEEDING BOUT		APPROXIMATE BODY TEMPERATURE RANGE	N (LIZARDS, FEEDING BOUTS)	RATE OF FEEDING ($\bar{X}$ GRAPES PER MIN)			MEAL SIZE (PERCENT BODY WEIGHT)		
				$\bar{X}$	SD	RANGE	$\bar{X}$	SD	RANGE
IA[1]	0850-1149	23.6-29.2	5,8	1.1[3]	0.6	0.4-2.0	4.0[4]	2.5	0.8-8.4
IB[2]	0850-1439	23.6-40.3	5,23	-	-	-	6.8	2.6	4.2-11.7
II[1]	1150-1300	34.8-40.3	4,11	2.3	1.1	1.1-5.0	7.0	0.9	5.7-8.3
III[1]	1458-1555	34.8-40.3	5,13	2.2	1.1	1.0-5.1	6.4	1.0	3.9-7.6

[1]Grapes consumed in a single feeding bout.

[2]Grapes consumed during the full day starting with the feeding bout in IA.

[3]Mean significantly lower than II and III ($p \leq 0.01$) by a one-sided *t*-test.

[4]Mean significantly lower than IB ($p \leq 0.025$) and II and III ($p \leq 0.005$).

feeding was undoubtedly reduced during tracking, transmitters also probably became lodged for variable times between the septa of the voluminous proximal colon. See Iverson (1980) for a description of *Cyclura*'s digestive tract.

Lizards most commonly defecated near the morning basking site during the regulating phase, on the average, 87 minutes after the first T_b maximum (SD = 104, N = 46, Figure 42). This was only 31.0 percent of the average time between the first and last maximum T_b's (292.1 minutes). Large solid objects, for example, far-field transmitters and hermit crab appendages, may be expulsed later in the day, on the average, than leaves and small seeds. Almost all defecations occurred at T_b's between 33.6 and 40.4 C ($\bar{X}$ = 37.6, SD = 2.17, N = 46). Even though fecal material was not found in lizard burrows, captive individuals occasionally defecated when handled at T_b's as low as 25 C. The defecation at a T_b of 27.0 C was by an untouched lizard which saw me while it was confined in the rooftop arena.

Drinking

Drinking was an infrequent behavior in *Cyclura*, even in captivity, where water was readily available. Drinking in free-ranging lizards was observed only once, in the dry month of February. An adult male licked a few drops of rainwater from the surface of dead sea grape leaves (*Coccoloba uvifera*) lying on the ground. Three of four caged lizards in June didn't drink until five, six, and seven days after capture and then only infrequently. The fourth did not drink at all during 12 days in captivity. Lizard 6 drank five times within an hour and a half, starting immediately after completion of egg laying

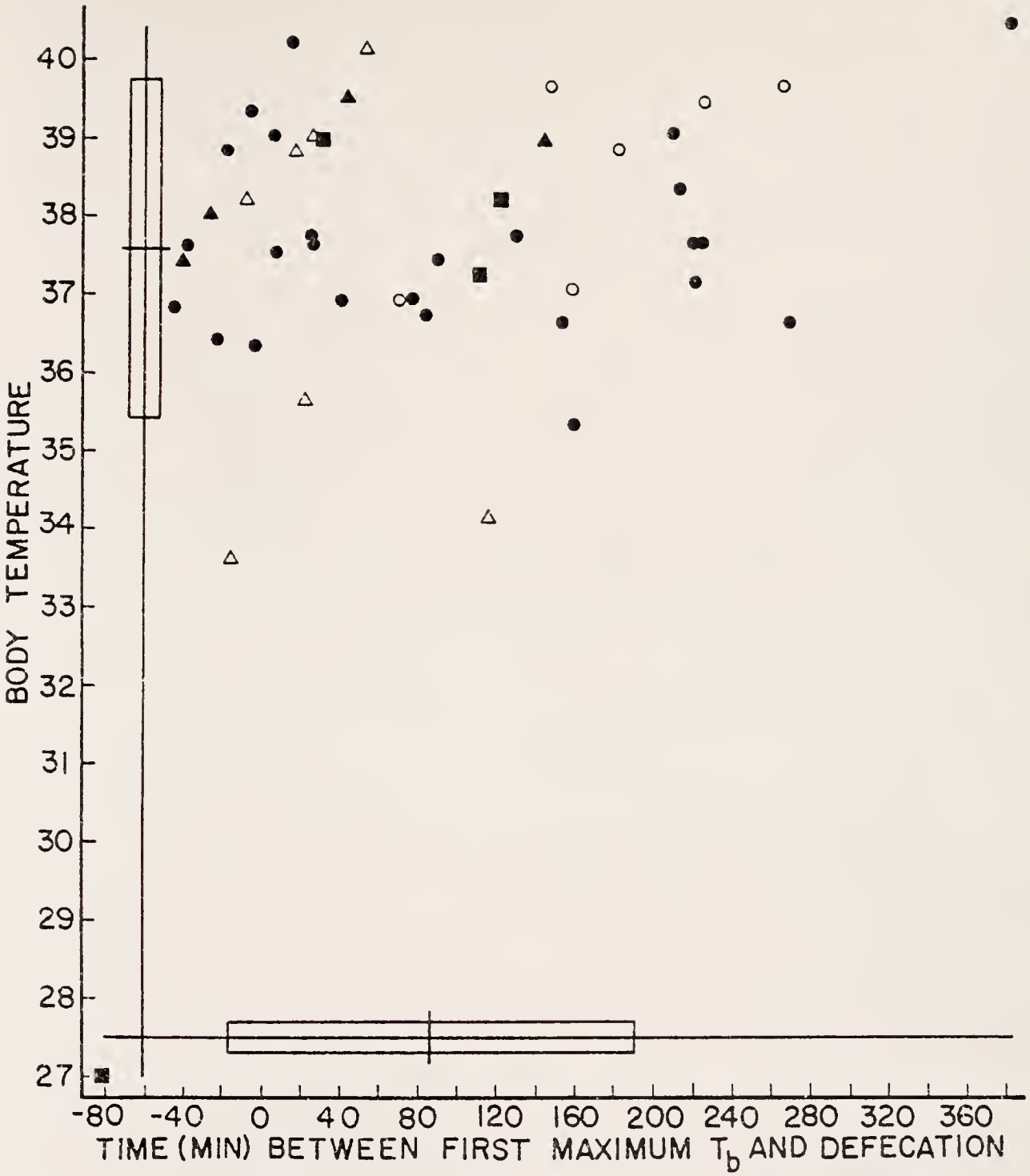


Figure 42. Defecation body temperatures and timing. Lizards defecated in the arena atop the zoology building (solid squares), field cages (solid triangles), field (free-ranging lizards defecating far-field transmitters; open circles), Gainesville pen (open triangles), and thermal gradients (solid circles). Means, plus and minus one standard deviation, and ranges for defecation timing and T_b are represented beside the abscissa and ordinate, respectively.

in the field cage. She drank only twice during the previous twelve days. Clearly, body water is normally primarily obtained from food rather than from free-standing sources. Drinking occurred at a mean T_b of 38.2 C (33.7-41.3, N = 15) in the June field cages.

Nasal Salt Gland Secretion

Nasal salt glands have been studied physiologically in members of six of nine iguanine genera: *Amblyrhynchus*, *Conolophus*, *Ctenosaura*, *Dipsosaurus*, *Iguana*, and *Sauromalus* (see Dunson 1976 for a review) and may in fact occur in all iguanines. Dissection revealed the gland's gross morphology to be similar to other iguanines. *Cyclura* could often be located in the field by listening for the sneezing sound made when the animals cleared accumulated gland secretion from their nostrils. A large male could propel secretion droplets up to a meter into the air and two meters to the side with a quick partial exhalation and somewhat semi-circular movement of its head. Iguanas usually sneezed while sitting still, most commonly just prior to walking. Marine iguanas also usually sneeze just prior to moving, as before changing basking positions or before entering the sea after morning basking (Carpenter 1966). The correlations may be anticipatory of an increased respiratory rate during movement. The hourly sneezing rates of two large males tracked in February were fairly constant throughout the day (N = 10 days, $\bar{X}$ = 2.85 sneezes/hr, ranges of daily $\bar{X}$'s = 1.98-3.82, SD = 0.73; range of sneezes/hr = 1-6). Actual rates were undoubtedly slightly higher, due to brief discontinuities in tracking contact and the limitations of human hearing in windy locations. Sneezing was restricted primarily to regulating phase T_b's ($\bar{X}$ T_b = 37.7 C, range = 29.1-40.9, SD = 1.66, N = 144 sneezes).

Time-Motion Study of Penned Lizards

Iguanas in the Gainesville pen spent most of their summer days just sitting. Active time averaged 1.8 percent of emergent time (Table 18). A log-log plot of mean daily distance traveled for individual lizards vs. confinement area was linear, with a significantly positive slope (Figure 43). Thus, active time was probably greater in the field. Percent active time in the field can be estimated using the following equation, assuming equal rates of movement in the field and pen:

$$A_f = A_p \cdot (D_f \cdot D_p^{-1}) \qquad (5)$$

where A_f and A_p are mean percent active times in the field and pen, respectively, and D_f and D_p are the mean daily distances traveled. The estimated A_f, 7.5 percent of emergent time, is about equal to the 8 percent maximum for the small ($\bar{X}$ = 240 g) herbivorous lizard, *Egernia cunninghami* (Wilson and Lee 1974).

Penned iguanas spent a higher percentage of their active time in thermoregulatory movement than free-ranging *Egernia* (43 vs. 12 percent). This was probably due to *Cyclura*'s higher mean operant T_b (37.5 vs. 32.9 C), coupled with the small amount of time direct sunlight was available in the pen, as well as the ease of obtaining food in the pen (an average of 41 vs. 85 percent of active time in pursuit of food). Thermoregulatory movements in the pen, consisting of shuttling walks and sun orientations, took less time per movement and occurred at higher rates per hour than either feeding or social behavior. Comparison of individual lizard results is not justified since both weather and activity periods varied considerably from day to day. However, as expected, the mean number of hourly thermoregulatory movements does appear to be inversely correlated with body weight.

Table 18. Time-motion study of *Cyclura carinata* in the Gainesville pen. Five lizards were observed for one day each in July. A movement unit is any complete behavioral sequence, such as a feeding bout, a chase, or a walk to the shade.

Lizard	1	2	3	4	5	$\bar{X}$
Weight (G)- Sex	1260-M	1240-M	1195-M	600-F	129	
Emergent Time (Min)	473	281	414	348	188	
Percent Pen Shade Time	45	47	37	33	5	
Percent Overcast Time	25	15	40	9	59	
Mean Sun Exposed Sand Temperature	40.7	31.4	31.7	38.0	42.2	
TOTAL ACTIVITY						
Active Time (Min)	10.6	2.6	7.2	6.8	4.0	6.2
Percent Emergent Time	2.2	0.9	1.8	2.0	2.1	1.8
Movement Units	87	49	70	108	101	83
$\bar{X}$ Hourly Movements	11.0	10.5	10.1	18.6	32.2	16.5
FEEDING						
Total Time (Min)	5.4	0.9	3.7	2.0	1.6	2.7
Percent Emergent Time	1.2	0.3	0.9	0.6	0.9	0.8
Percent Active Time	51	33	51	30	41	41
Total Movement Units	29	8	17	20	8	16
$\bar{X}$ Hourly Movements	3.7	1.7	2.5	3.4	2.6	2.8
$\bar{X}$ Seconds/Movement	11.2	6.4	12.9	6.0	12.2	9.7
SOCIAL BEHAVIOR						
Total Time (Min)	3.2	0.2	0.5	1.8	0.3	1.2
Percent Emergent Time	0.7	0.1	0.1	0.5	0.2	0.3
Percent Active Time	31	8	6	26	8	16
Total Movement Units	15	5	3	17	15	11
$\bar{X}$ Hourly Movements	1.9	1.1	0.4	2.9	4.8	2.2
$\bar{X}$ Seconds/Movement	13.0	2.4	9.3	6.2	1.2	6.4
THERMOREGULATORY BEHAVIOR						
Total Time (Min)	1.9	1.5	3.1	3.0	2.0	2.3
Percent Emergent Time	0.4	0.6	0.8	0.8	0.9	0.7
Percent Active Time	18	59	43	44	51	43
Total Movement Units	43	36	50	71	78	56
$\bar{X}$ Hourly Movements	5.5	7.7	7.2	12.2	24.9	11.5
$\bar{X}$ Seconds/Movement	2.6	2.6	3.7	2.5	1.6	2.6

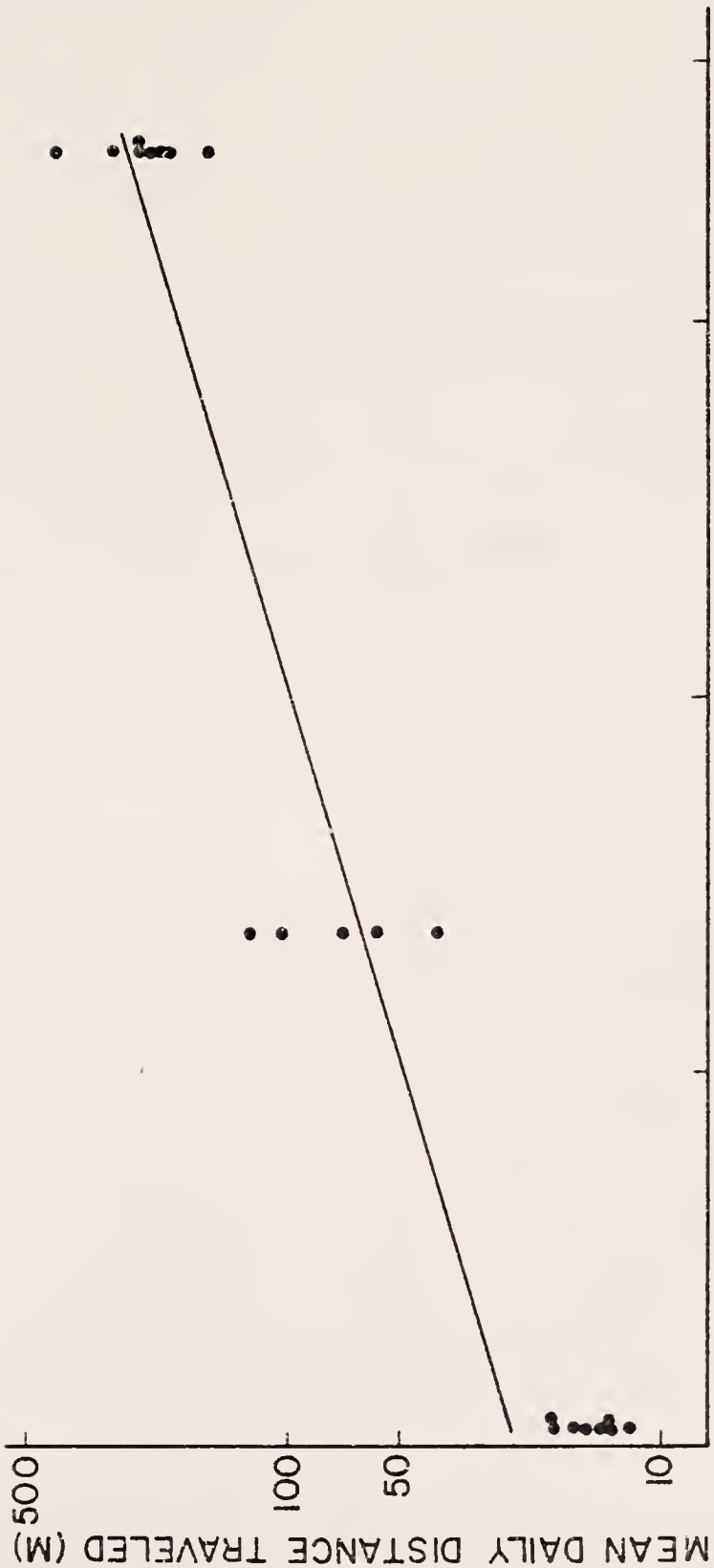


Figure 43. Correlation of lizard mobility with confinement area. The mean daily distance traveled was measured for adult lizards in the thermal gradient (N = 4 lizards, Dec-Jan), Gainesville pen (N = 5, July-Aug), and Field Site II (N = 4, Oct). Confinement area in the field was defined as the mean home range size. The linear regression equation fitted to the data was; Log Y = 0.297 Log X + 1.398 (N = 22, r = 0.957, $p \leq 0.0005$).

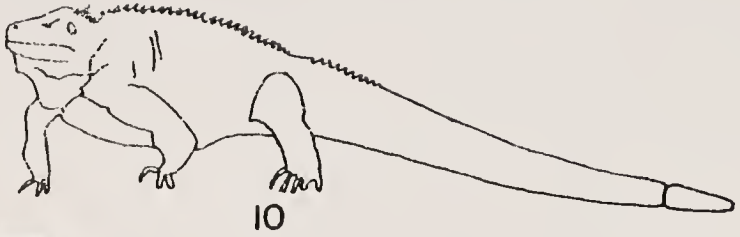
Behavioral Thermoregulation

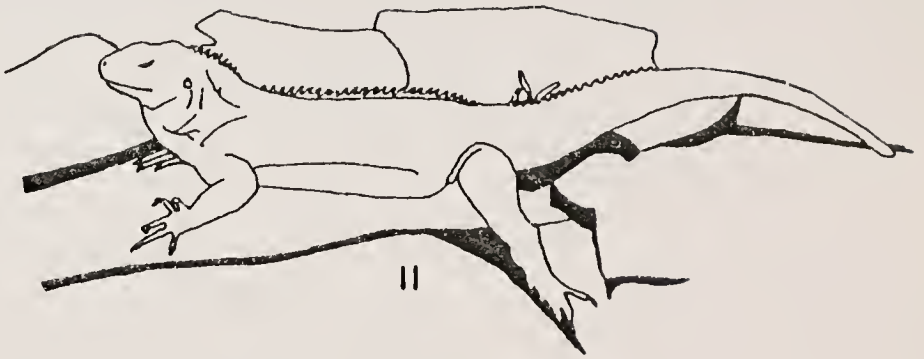
Description of Thermoregulatory Movements and Postures

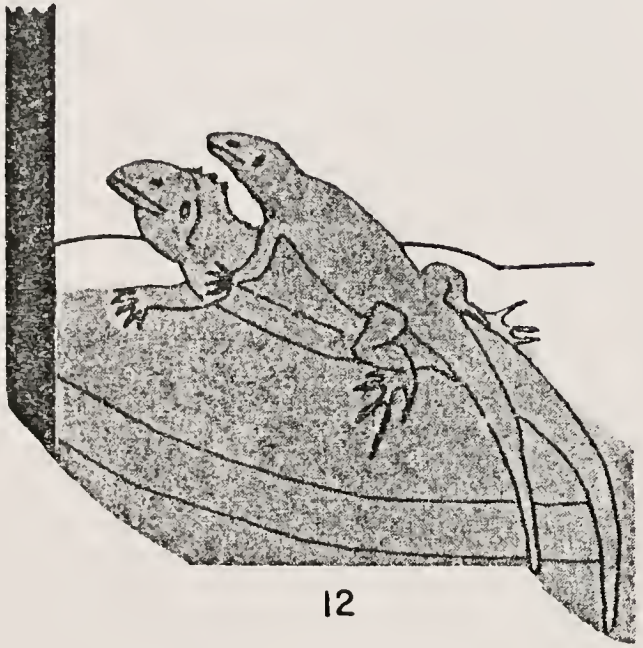
When a lizard assumes a characteristic posture or moves its body in a consistent way in a specific microclimate, resulting in a predictable decrease, increase, or stabilization of peripheral or core T_b, the behavior is probably thermoregulatory. However, care must be taken when assigning a single feeding, social, or thermoregulatory function to a behavior, since multiple functions are likely. For example, an arboreally feeding lizard may originally have climbed a bush to avoid a hot surface microclimate. Possible nonthermoregulatory functions of thermoregulatory behaviors will be mentioned where appropriate in the following descriptions. Numbers in parentheses refer to illustrations in Figure 44.

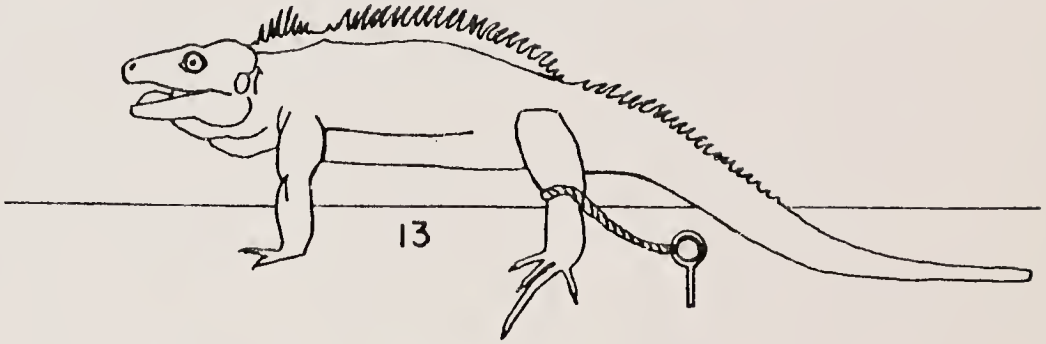
Pre (1) and Partial (2) Emergence Postures. The preemergence pause occurred as the lizard rested in sight of the burrow mouth, usually just inside the lip. The pause was a very consistent behavior, never omitted in the Gainesville pen. Lizards secured information about the outside world without exposing themselves to unfavorable weather or possible danger. Emergence was delayed by overcast skies, presumably due to low light intensity inhibition, and by unfamiliar noises such as a human voice. Partial emergence permitted a visual scan of the immediate burrow area, again with minimal danger to the lizard. The behavior is analogous to partial emergence from the water prior to basking in semiaquatic turtles. However, no unsolicited head rotations were noted, as have been observed in *Chyrsemys scripta* (Auth 1975). When frightened, lizards either turned quickly around and retreated head first into the

Figure 44. Thermoregulatory motions and postures of *Cyclura carinata*. Illustrations were made from photographs taken in the field (3, 8, 9, 10; free-ranging lizards, 14; captive lizard), Gainesville pen (1, 2, 4, 11, 12, 13), and laboratory temperature control chamber (5, 6, 7).









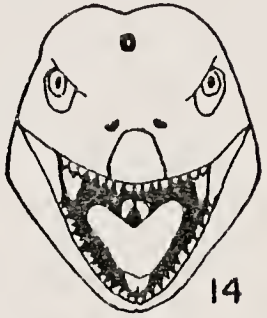


Figure 44. Continued.

burrow or backed in tail first. Head heating may occasionally be significant, for example, during a slow emergence at low T_b. Sand burrow mouths were located below the ground surface in the side of an inverted cone. Due to greater indirect radiation from the sides of the cone, higher substrate temperature, and lower wind velocity, lizards emerging into the cone, especially near midday, probably heated faster than animals moving immediately to level ground. However, since burrow mouths were often located in the shade, initial head heating was not a consistent populational requirement.

Upright Posture (3,5). The forelegs were adducted toward the thorax and variably extended, keeping the ventral pectoral region and abdomen off the substrate, as far back as the pelvic girdle. The forelegs were straight in a maximally upright animal, and the head was higher off the substrate than illustrated in (3). The hindlegs sprawled laterally. The tail was flat on the ground except when curved directly upward in an apparent appeasement display by females and subdominant males. Lizards assumed the upright posture more frequently than any other. It was observed consistently during the morning heating phase, commonly during pauses between foray walks, and commonly during summer middays when lizards sought out areas exposed to the easterly wind. Lizards appeared to be maximally alert, rarely closing their eyes for longer than a second. They assumed a maximally upright posture when hearing an unusual noise, seeing an unfamiliar object moving into the field of view, or looking over an obstruction. Substrate contact also varied with air, body, and substrate temperatures (see Thigmothermia). For example, the lizard in (5) minimized contact with a cold photothigmotron substrate while in warm air (T_b = 30.2 C, T_s = 21, T_a = 37.6).

Prostrate Posture (4,6). Maximum relaxation on a flat substrate was characterized by lateral expansion and dorso-ventral compression of the trunk. When viewed from the side, the midsagittal crest was slightly concave to slightly convex. Undisturbed lizards occasionally relaxed their heads on the substrate. Lizards were less alert than in the upright posture, as indicated by intermittent eye closure. The position of the legs varied with radiant input, substrate temperature, and probably, wind velocity. For example, the lizard in (4) was cooling slowly in the late afternoon shade while relaxing on a concrete block. Substrate temperature averaged 2 C less than the lizard's core, which was in the regulating range. Contact of the legs with the trunk and tail minimized conductive and radiative heat loss. In contrast, the legs of the lizard in (6) extended out from the body and made maximum contact with the substrate, since substrate temperature in the photothigmotron was higher than both the still air and the body core (T_s = 41, T_a = 29, T_b = 36.2 C). The prostrate posture was assumed during overcast following clear skies, with T_b in the regulating range and stable or slowly decreasing, and during the late afternoon in diminishing sunlight, with T_b commonly at the highest point during the day. The posture was also commonly assumed by subdominant males when approached by a dominant male, a sign of submission which probably reduced the probability of a chase.

Positive Normal Orientation (7). The lizard maximized the body surface area exposed to a radiant heat source by orienting

perpendicularly (normal orientation)[1] and curving its body slightly toward the source, in this case, a heat lamp in the photothigmotron. The angle of incidence of the radiation was normalized by tilting the sun exposed side toward the heat lamp (positive orientation). The right side of the lizard's trunk in (7) constituted 67.1 percent of the total trunk photographic area.

Object Utilization During Sun Orientation. Lizards maximized radiant input by facing away from the sun while propped up anteriorly on a rock or some other object (positive parallel orientation). This behavior was fairly common in the early morning during the cooler months of the year. It was rarely observed during the summer, when lizards usually assumed an upright posture during morning basking, on level ground and approximately perpendicular to the sun's rays. In the late afternoon at Site II, lizards commonly sat on the sides of hills which faced the sun. Minimizing radiant heat input by orienting negatively parallel to the sun was rarely observed in the field, probably due to the large areas of shade present at both Sites I and II.

---

[1] Heath's terminology (1965) describing lizard sun orientation has been used in the present paper. It is based on whether the radiated dorsal body surface of the lizard faces toward (positive) or away from (negative) the sun and whether the long axis of the lizard's body is perpendicular (normal) or parallel to the incoming parallel rays of the sun. Brattstrom's (1971) and Greenberg's (1977) schemes were rejected due to their use of positive and negative orientations to describe how the lizard's head is oriented with respect to the sun, which seems less logical than using the terms in relation to the dorsal body surface. Brattstrom also confuses body posture (the position of the lizard's head, trunk, and tail with respect to the substrate and the position of the limbs with respect to the trunk) with body orientation to the sun; for example, in his "extreme positive orientation." Greenberg's scheme was also rejected because he had to invent a second set of terms to describe the positive normal orientation. Muth's scheme (1977b), quite different from the three above, is the most mathematically precise, taking into account all intermediate orientations. It is admirably suited to computer simulations but was not adopted for the present study since solar zenith angles were not measured and most of the literature descriptions also lack the required quantification for conversion to his terminology.

Arboreal Climbing (9). This behavior was probably thermoregulatory in *Cyclura*, removing the lizard from excessive heat inputs at ground level in the summer and from low ground surface temperatures in the winter. However, the mean T_b change of arboreally feeding lizards at Site II in October was not significantly positive. Unfortunately, I have no June-July nor December-January data. Iverson (1977) observed considerable winter arboreal climbing without feeding at his Pine Cay field site. Lizards sat quietly on branches in the sun.

Walking (10) and Running. *Cyclura* moved at essentially three speeds; a slow walk, a medium speed trot or slow run, and a fast run. Walking and slow running correspond to Type A locomotion and fast running to Type B locomotion in *Uromastix aegyptius* (Dmi'el and Rappeport 1976). Walking was the most common locomotory mode used during forays. A considerable length of the distal tail made contact with the substrate, and the ventral trunk was minimally elevated above the ground. Walking was restricted to substrates with surface temperatures below approximately 45 C. Slow running occurred when I approached lizards too closely while tracking, when a female or subdominant male increased its distance from an approaching dominant male, and when any lizard crossed large exposed areas with surface temperatures in excess of 45 C. Fast running, which was always quadrupedal, occurred during territorial chases and escapes from potential predators. The tail extended horizontally off the ground, and the ventral body surface was maximally elevated.

Semiprostrate Posture (11). Body contact with the substrate extended from the pectoral girdle nearly to the tip of the tail, with considerable lateral expansion of the trunk. The calves were directed

diagonally toward the tail (3) or sprawled laterally (11), especially when the substrate sloped downward laterally. Judging from results in the Gainesville pen, lizards assumed a semiprostrate posture during the morning basking phase only when substrate temperature exceeded core body temperature. The posture was also assumed during the regulating phase in either the sun or the shade. However, substrate temperature was neither consistently higher nor lower than body temperature.

Shade Seeking (12). Lizards sought out shaded microclimates when body temperatures extended into the maximum body temperature range. Brief physical contact was made between two or three iguanas during shade seeking in the Gainesville pen, a behavior never observed in the field in a thermoregulatory context, where lizard density was much lower and shade was less limited. In (12) a subdominant adult female had crawled onto the back of an adult male. Soon after the photograph was taken the male left the shade to the female by sliding forward and walking away. The subdominant usually licked the dominant once or twice on its dorsal surface before mounting. Subdominants moved away from dominants before body contact could be made.

Lizards sitting partially in the shade during midday hours eventually moved exposed portions of their bodies into the shade; for example, curved their tails or their heads, as the male in (12).

A little less than half the Gainesville pen was continually shaded. It was infrequently traversed during daily lizard movement. When rock piles and shelters were rearranged, activity considerably increased for a day or two. Lizards walked further and explored the entire pen. New areas were subsequently excluded from daily travel.

Captives undoubtedly became familiar with the new locations of thermally suitable microclimates during this exploratory phase.

Elevated Posture (13). This posture was characteristic of heat stressed lizards and was usually accompanied by intermittent or continuous panting. Legs were extended, maximally raising the trunk off the hot substrate. The trunk was flattened ventrally via lateral expansion, possibly reducing heating by radiation reflected off the ground (Norris 1967). Elevation also enhanced forced convective cooling and moved the lizard into a zone of lower air temperature. Heat stressed lizards were never seen in the field; the 1900 g dominant male in (13) would probably never reach the panting setpoint as a free-ranging animal.

Feeding lizards on the ground often assumed a mildly elevated posture, perhaps aiding in swallowing. Adult males elevated their trunks during territorial face-offs. The trunk was laterally compressed rather than laterally expanded as during panting.

Panting (13,14). The mouth was not opened maximally during panting. The tongue was elevated, engourged with blood, and extended to the edge of the mandible. The eyes bulged perceptibly. Air flow over the tongue and roof of the mouth of lizards staked out in the summer sun resulted in sufficient evaporative cooling to decrease the heating rate of the large intestine as well as the head.

Substrate Penetration with the Legs. This behavior was observed only once, in an adult caged male given no access to shade. While in a walking position, the lizard repeatedly pushed forward with its rear legs while extending its forelegs into the cool, loose subsoil (T_b = 38.0, T_s at the surface = 44.0 C). As body temperature fell to between

36.9 and 36.1 C during the following overcast period, the behavior was repeated several times, presumably to reach the now warm subsoil.

Sand Swimming. When crossing hot, loosely arranged sands, such as on bulldozed roads, lizards occasionally crawled forward (for short distances) with maximum ventral substrate contact, using both fore and hind legs for locomotion. Presumably, this behavior maximized body and limb contact with cooler subsurface sand.

Reflexion of the Digits. While pausing on hot exposed substrates in either the upright, semiprostrate, or walking postures, lizards commonly reflexed their digits soon after stopping, making contact with the substrate with only palmer and plantar surfaces of the feet. Lizards soon moved to the shade rather than elevating their feet completely off the substrate.

Substrate Rubbing and Touching. Some of the following behaviors may have a temperature sensing function: 1. sand swimming. 2. ventral body surface rubbing. Lizards rubbed their ventral trunks on rocks or other hard objects, sometimes dragging themselves short distances forward using their forelegs while extending their rear legs posteriorly. The behavior was most commonly observed just prior to a walk during a foray and just before evening submergence. 3. chin rubbing. The sides of the jaw were alternately rubbed on rocks or branches, most commonly immediately before walking after a lengthy pause. 4. substrate licking. Besides its olfactory and gustatory functions, licking may convey surface temperature information. Lizards commonly licked a site before sitting on it, especially in the Gainesville pen. The presence of both cold and heat receptors in the tongue of the domestic cat has been

demonstrated by recording spike potentials of the lingual nerve (see Zotterman 1953 for a review).

Shuttling Behavior

The four caged adults observed in the field in June had mean shuttling movement rates of 2.31, 2.43, 3.04, and 4.80 per hour (Lizards 6, 4, 7, and 5; body weights of 815, 645, 1290, and 723 g, respectively). Lizard 5 shuttled at a significantly higher rate than the other three animals. Since rates were not significantly different in the simple and complex habitats, all data for each lizard were pooled. Shuttling rate was inversely related to the standard deviation of mean body temperature (SD = -0.148 Shuttling Rate + 1.59, r = -0.394, $p \leq 0.05$). Thus, increased T_b stability required more shuttling and, presumably, a higher energy expenditure. The graphs in the upper part of Figure 45 illustrate a day's shuttling at about the average rate and at the maximum observed rate.

The time caged lizards spent in direct sunlight, vegetational shade, and burrows varied with the hour of the day (lower graph, Figure 45). Summer peaks of direct sunlight exposure at 0800-0900 and 1600-1700 bracketed the free-ranging lizard activity peaks at 0900-1100 and 1400-1600 (Figure 37). Direct sunlight peaks moved closer to one another as winter approached, with a single midday peak in the coldest months of December and January. The degree of heliothermy, as measured by the percent sun exposure time of a lizard on a clear day, ranged from 27.7 to 65.7 percent (N = 21 June days, $\bar{X}$ = 42.5, SD = 9.49) and was directly related to mean body temperature ($\bar{X}$ T_b = 0.086 Percent Emergent Time in the sun + 35.58, r = 0.406, $p \leq 0.05$). Only 18.9

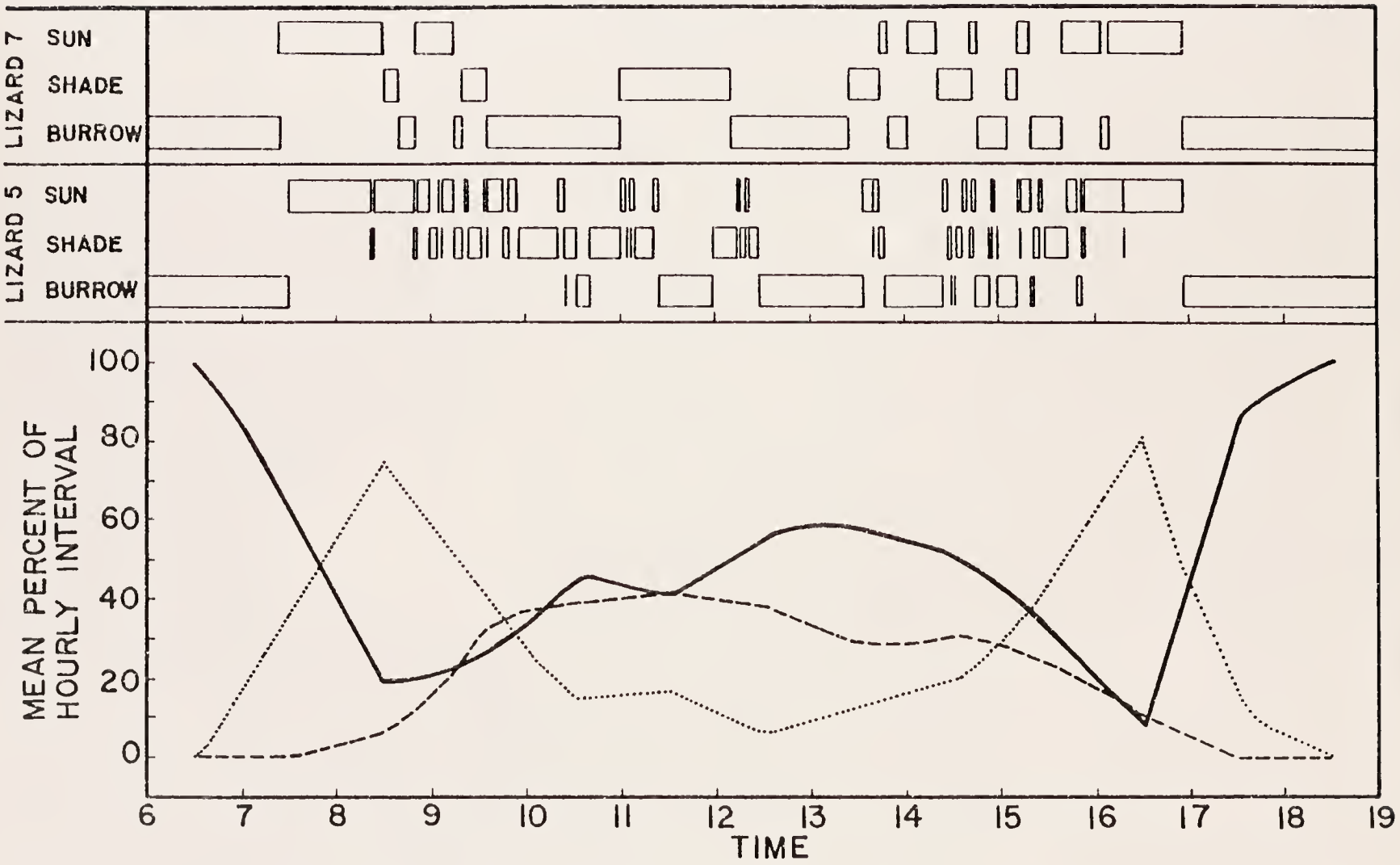


Figure 45. Lizard shuttling in the summer field cages. In the upper graph, movements of an average shuttler (Lizard 7 on June 26, $\bar{X}$ = 2.6 shuttles/hr) and a fast shuttler (Lizard 5 on June 27, $\bar{X}$ = 7.2 shuttles/hr) between sun exposed, vegetationally shaded, and burrow portions of the cage are illustrated The mean percentages of each hour spent in the sun (dotted line), vegetational shade (dashed line), and burrow shade (solid line) are illustrated in the lower graph (for four lizards each monitored for three days).

percent of the daily direct sunlight time was distributed between 1000 and 1500. During the hottest part of the day, lizards selected burrow shade significantly more of the time than the warmer vegetational shade (1300-1359, $p \leq 0.025$; 1400-1459, $p \leq 0.05$, one-sided t-test). Air temperature between 1200 and 1600 averaged 29.5 C (28.0-30.6) in the burrow and 34.9 C (32.9-37.5) in the vegetational shade.

Pianka (1969) found a direct relationship in fourteen species of *Ctenotid* skinks between the ratio of hindleg length to snout-vent length (HLL/SVL) and the percentage of the time lizards were first sighted in the open (PTSO). The HLL/SVL ratio decreased ontogenetically in *Cyclura carinata* (HLL/SVL = -0.00048 SVL + 0.7206, N = 26 lizards, HLL/SVL range = 0.70 - 0.54 SVL range = 89 to 332 mm, $r = -0.804$, $p \leq 0.0005$). If *Cyclura* fits the *Ctenotus* pattern, its ontogenetic range of HLL/SVL, 0.70 to 0.54, corresponds to a PTSO of 84 to 33 percent (HLL/SVL = 0.0031 PTSO + 0.438, N = 14 species of *Ctenotus*, $r = 0.769$, $p \leq 0.005$). Unfortunately, this was not checked in the field. However, the 42.5 percent mean time in the sun for the June caged *Cyclura* corresponds to a HLL/SVL ratio of 0.57 using the *Ctenotus* equation. The actual mean SVL for the four lizards, 275 mm, corresponds to a HLL/SVL ratio of 0.59, about equal to 0.57. The range of adult *Cyclura* HLL/SVL ratios places the species in the open area forager category of *Ctenotus* (6 of 14 species).

Free-ranging lizards utilized the wind as well as the shade to cool themselves during the hottest days. For example, Lizard 3, on returning from a foray at midday or early afternoon at Site II in February and October, often walked to a wind exposed ridge near its home burrow and sat in the shade in an upright posture. T_b stabilized

or declined during this period. The lizard did not orient its body in any consistent direction with respect to the wind.

Core T_b at shade seeking varied in a regular fashion during the day (Figure 46). Each of the four caged lizards moved into the shade at a low hourly mean T_b during the hottest part of the day. The daily ranges of hourly mean T_b's for shade seeking were 2.4, 1.7, 1.6, and 1.5 C ($\bar{X}$ = 1.8 C). The corresponding depressions in the mean T_b's for sun seeking were about the same: 2.9, 1.5, 1.5, and 1.3 C, respectively ($\bar{X}$ = 1.8 C) and also maximized between 1200 and 1300.

Sun Orientation

Direct radiative heat input from the sun increases as a lizard's shadow area increases (Heath 1965). With a single heat lamp directed at 45° below the horizontal onto the photothigmotron substrate, an iguana could maximize shadow area by assuming an approximately normal orientation and tilting the closest side of its trunk toward the heat lamp (positive normal orientation) or facing directly away from the lamp and maximizing forebody elevation (positive parallel orientation). Radiant input could be minimized by assuming a normal orientation and tilting the trunk away from the heat lamp (negative normal orientation) or by facing directly toward the lamp and maximizing forebody elevation (negative parallel orientation). Of course, lizards could also change heat input by moving closer to or farther away from the heat lamp. *Cyclura* maximized its shadow area in and below the T_b range for morning emergence (Figure 47). The greatest shadow area was recorded at the lowest substrate temperature (the lizard was approximately the same distance from the heat lamp during the early stage of heating at all

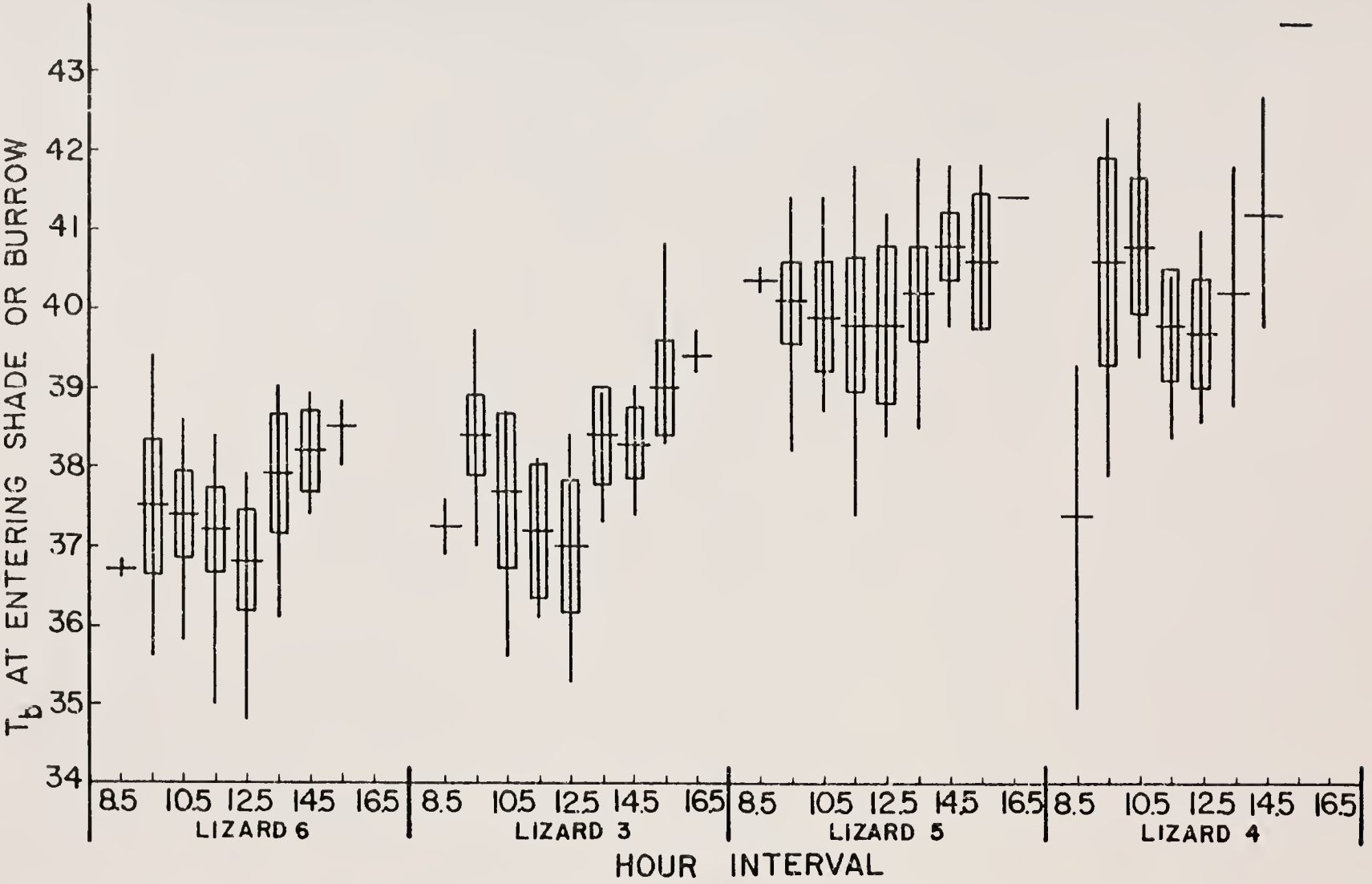


Figure 46. Midday depression of shade seeking body temperature. T_b's have been averaged for hourly intervals over five day periods for each of four caged lizards monitored in the field in June. Only T_b's which were followed by intervals of five minutes or longer in burrow or vegetational shade have been used to calculate the means. Horizontal lines are means, vertical lines; ranges, and rectangles; plus and minus two standard errors of the mean.

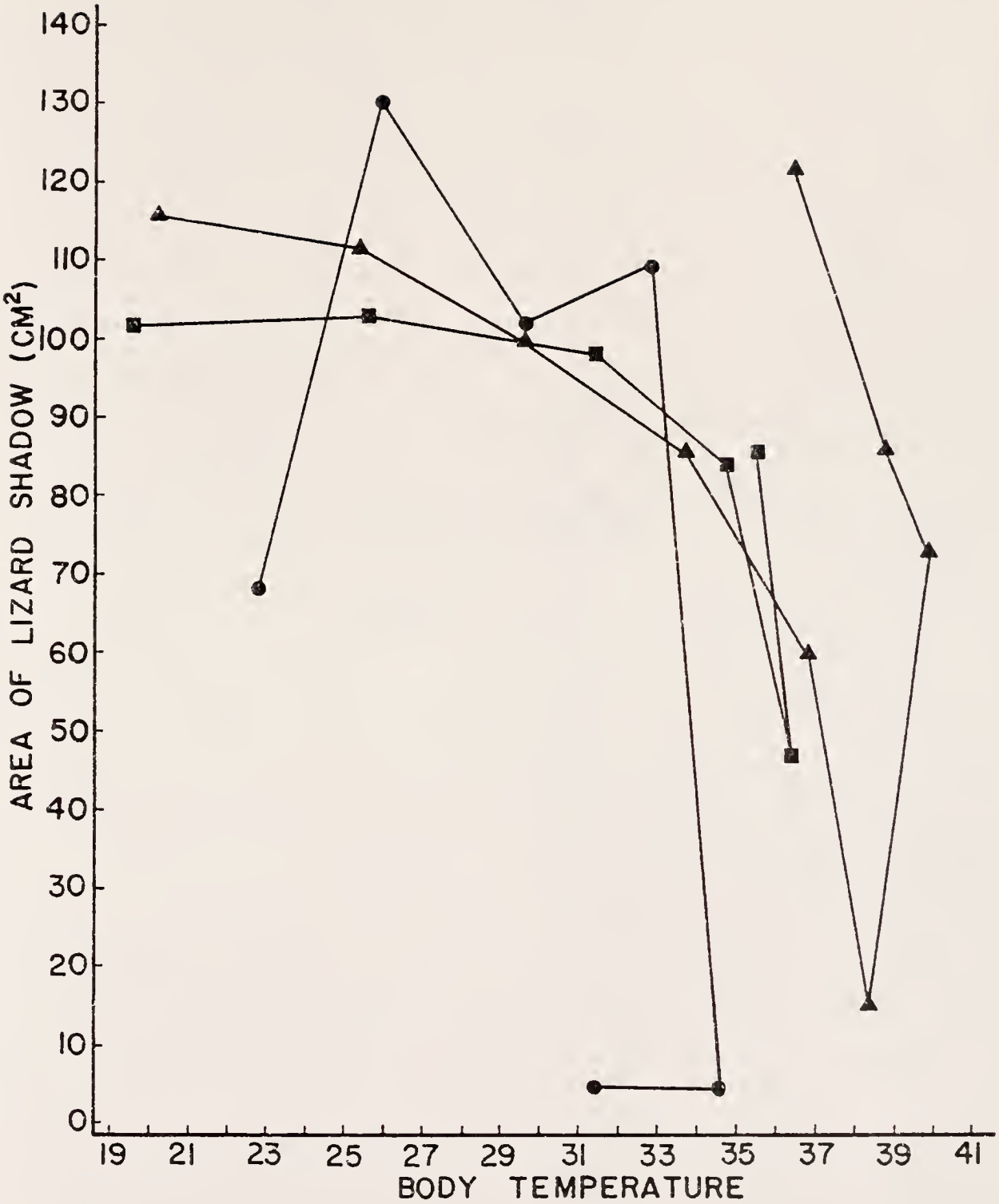


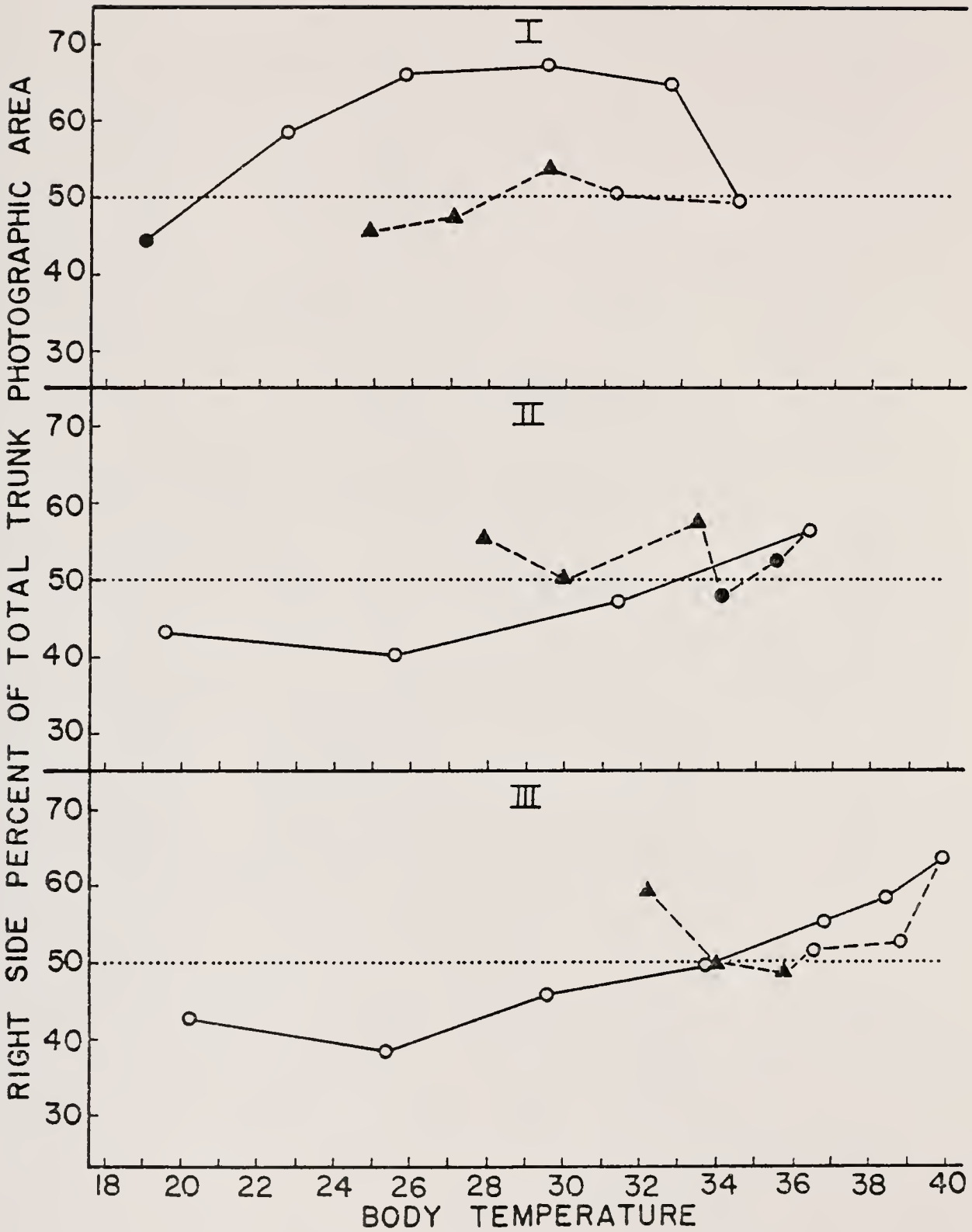
Figure 47. Lizard orientation to a heat lamp during heating and cooling in the photothigmotron. Three records for a 985 g female are illustrated, one each at substrate temperatures of 20 C (circles), 31 C (squares), and 38 C (triangles). Air temperature was constant at 19 C during the three runs.

substrate temperatures). The iguana either abruptly or gradually reduced its shadow area as T_b increased. The greatest decrease in area per °C rise in T_b occurred as the mean preferred T_b was approached (37.0 C). During the experimental run at a substrate temperature of 38 C, the lizard walked away from the heat lamp when T_b reached 39.1 C, maximizing its shadow area again as T_b declined to 36.5 C at the greater heat lamp distance.

The occurrence and degree of positive and negative tilting orientations depended on body and substrate temperatures. The lizard in Figure 48 tilted positively while heating radiatively on the cold substrate (20 C) and negatively while receiving heat inputs from both the substrate (31 and 38 C) and the heat lamp. Tilting essentially ceased when the lamp was turned off. Curving the trunk toward (Figure 44, Illustration 7) or away from the heat source accompanied positive and negative tilting orientations, respectively. Curving also commonly occurred during parallel orientation.

Blindfolded iguanas neither tilted their trunks nor rotated their bodies during heating in the sun. Lizard contact with the substrate did increase with increasing T_b, however. Sun orientation appears to be mediated through the eyes rather than through temperature receptors heating at different rates in different areas of the dorsal integument. White (1973) came to the same conclusion regarding *Amblyrhynchus cristatus*. He could get the lizard to disregard the position of the real sun and reorient toward a concave mirror directing the sun's rays at the lizard's head.

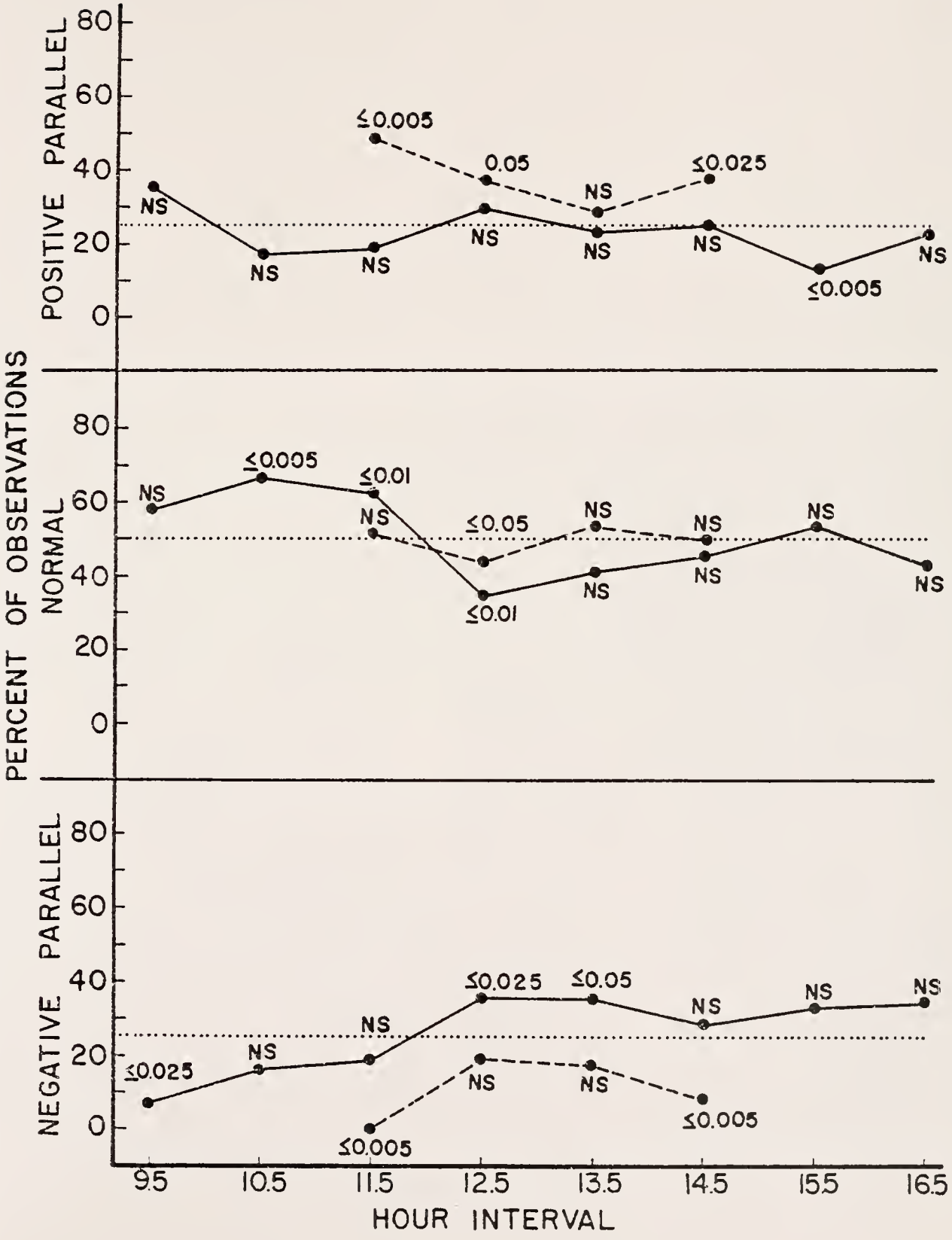
Figure 48. Positive and negative orientation (trunk tilting) during lizard heating and cooling. The three experimental runs were the same as illustrated in Figure 47. Substrate temperatures were 20 C (I), 31 (II), and 38 (III). The right and left photographic areas of the neck plus trunk were measured from photographs taken directly above the lizard. Points falling on the dotted line signify the lizard was in a bilaterally symmetrical posture, with equal right and left side photographic areas. The right side was either facing the heat lamp (open circles), facing away from the lamp (solid circles), or the lamp was turned off (solid triangles). The animal was either heating (solid lines) or cooling (dashed lines).


I
II
III
70
60
50
40
30
RIGHT SIDE PERCENT OF TOTAL TRUNK PHOTOGRAPHIC AREA
18
20
22
24
26
28
30
32
34
36
38
40
BODY TEMPERATURE

Iguanas changed their pattern of sun orientation both during the day and the year (Figure 49). Morning basking in the fall, as well as in the spring and summer, commonly occurred while in a perpendicular orientation. Lizards more commonly oriented positive parallel in the winter, presumably due to the increased declination of the sun. Object utilization during early morning and late afternoon basking also increased in winter. Negative parallel orientation, the minimum heat intake position, became significant during the hottest part of the day in the fall, but remained below chance expectation at all times in winter. Clearly, heat gain orientation was more common in the winter than the fall, where it was restricted to the morning hours. However, had the autumn pen not been totally shaded by 1645, the late afternoon increase in perpendicular orientations may have been sufficient to increase the 1500-1600 hour Chi-square to a significant level.

Cyclura has a large proximal colon, usually containing in excess of 40 percent of the digestive tract volume, located next to the left anterior abdominal wall (Iverson 1977). Does the animal preferentially heat this area, by orienting its left side perpendicularly toward the sun more than its right side? No significant difference was found between left vs. right side orientations when each full day's, body half data were simply summed and compared. However, when the frequency distributions were compared, the left side was favored in orientations between 68 and 121° in September and between 95 and 166° in December-January (Figure 50, $p \leq 0.05$, Wilcoxon signed rank test) in the Gainesville pen. The pen data for the warmer month of August showed no significant pattern. The left side predominance in the perpendicular range was greatest during morning heating, both in the September and

Figure 49. Daily and seasonal variation in sun orientation in the Gainesville pen. Instantaneous sun orientations were determined four times per hour for ten adult lizards during four clear days in September (solid lines, $\bar{X}\ T_a$ in the shade during lizard activity = 30.4 C) and one day each in late December and early January (dashed lines, $\bar{X}\ T_a$ shade = 23.0 C). Dotted lines are expected percentages based on chance. Possible significant differences of percentages from random expectation were tested for using Chi-square.


PERCENT OF OBSERVATIONS
POSITIVE PARALLEL
NORMAL
NEGATIVE PARALLEL
80
60
40
20
0
≤0.005
0.05
≤0.025
NS
≤0.01
≤0.05
9.5
10.5
11.5
12.5
13.5
14.5
15.5
16.5
HOUR INTERVAL

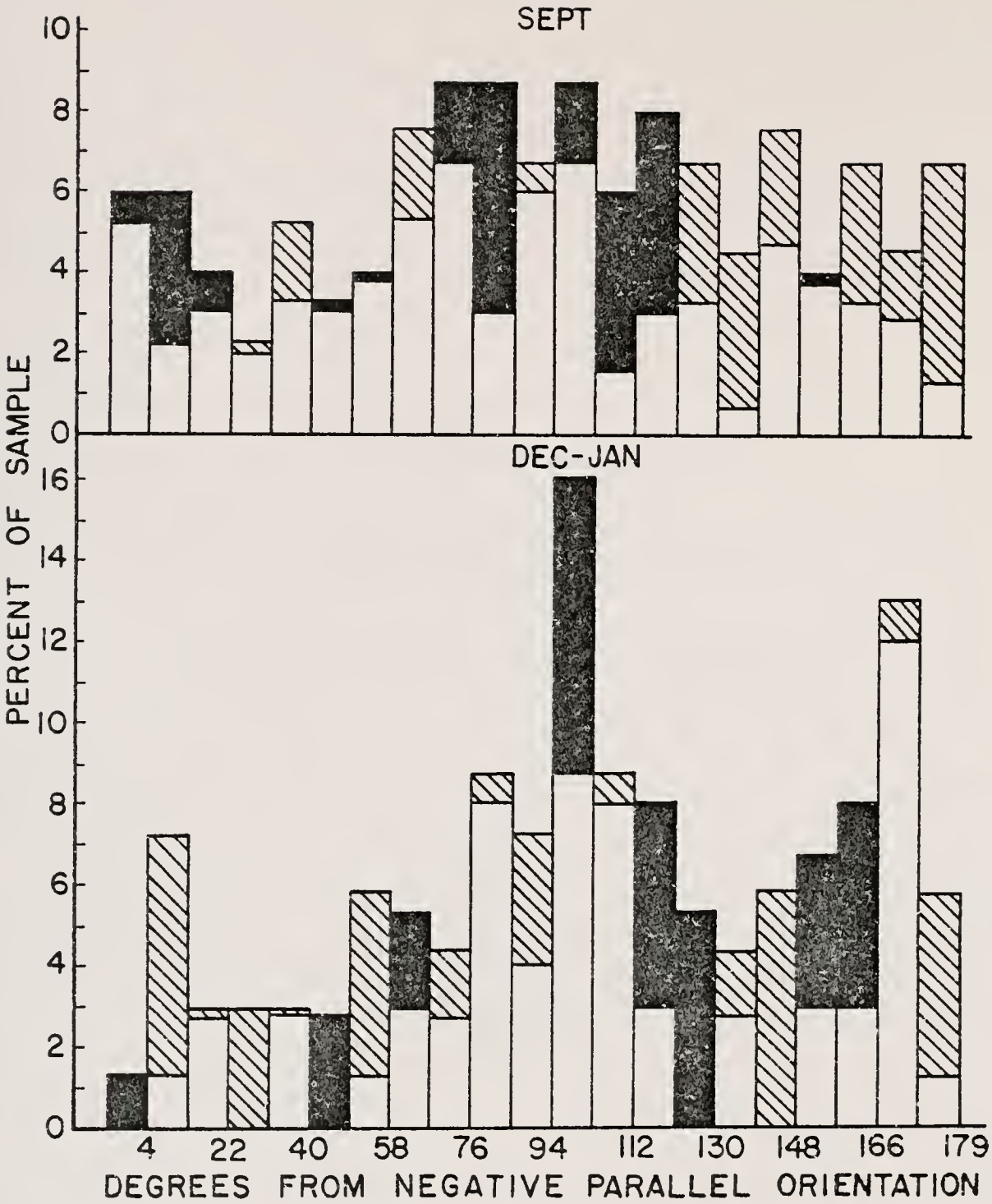


Figure 50. Left vs. right side sun orientation in the Gainesville pen. Instantaneous sun orientations were determined four times each hour for ten adult lizards during four clear days in September (N = 271 measurements) and one day each in late December and early January (N = 145). The orientations were arranged according to whether more of the left (shaded bars) or right side (diagonal hatching) of the lizard's trunk faced the sun.

December-January pen study and in a caged field iguana in October. Thus, it does appear that the proximal colon was preferentially heated. However, more data on free-ranging iguanas should be collected.

Another interesting finding, which may be related, comes from February and October tracking. Iguanas moved predominantly in clockwise, approximately linear, and counterclockwise paths during morning, midday, and afternoon hours, respectively (Figure 51). The orientation change was probably related to the changing sun position in the sky. Thus, with the sun at a southerly declination, a lizard had its left side facing the sun as it moved clockwise on its first foray, when, presumably, differential heating would be most necessary, especially if it were also important in the defecation response.

Integumental scales are imbricate over much of the body surface of *Cyclura carinata*. When heated from directly anterior and posterior to the overlapping scale edges, the posterior heating rates of dried skin patches often exceeded the anterior rates at equal angles of heat lamp orientation (Table 19). Skin patches from the ventral abdomen and the dorsal distal hindleg (1,2), with little scale overlap, heated at about the same rate at each anterior-posterior pair of equal radiation incidence angles. A/P ratios were higher in patches with more imbricate scales (3-6). It is of some interest that the scales of the ventral proximal tail had the greatest A/P ratios, yet receive mostly thermal radiation from the substrate rather than direct solar radiation.

Regal (1975) demonstrated for *Dipsosaurus dorsalis* and *Sceloporus magister* that imbricate scales act as miniature radiant heat shields by producing a shadow zone underneath the overlapping edges. Unlike

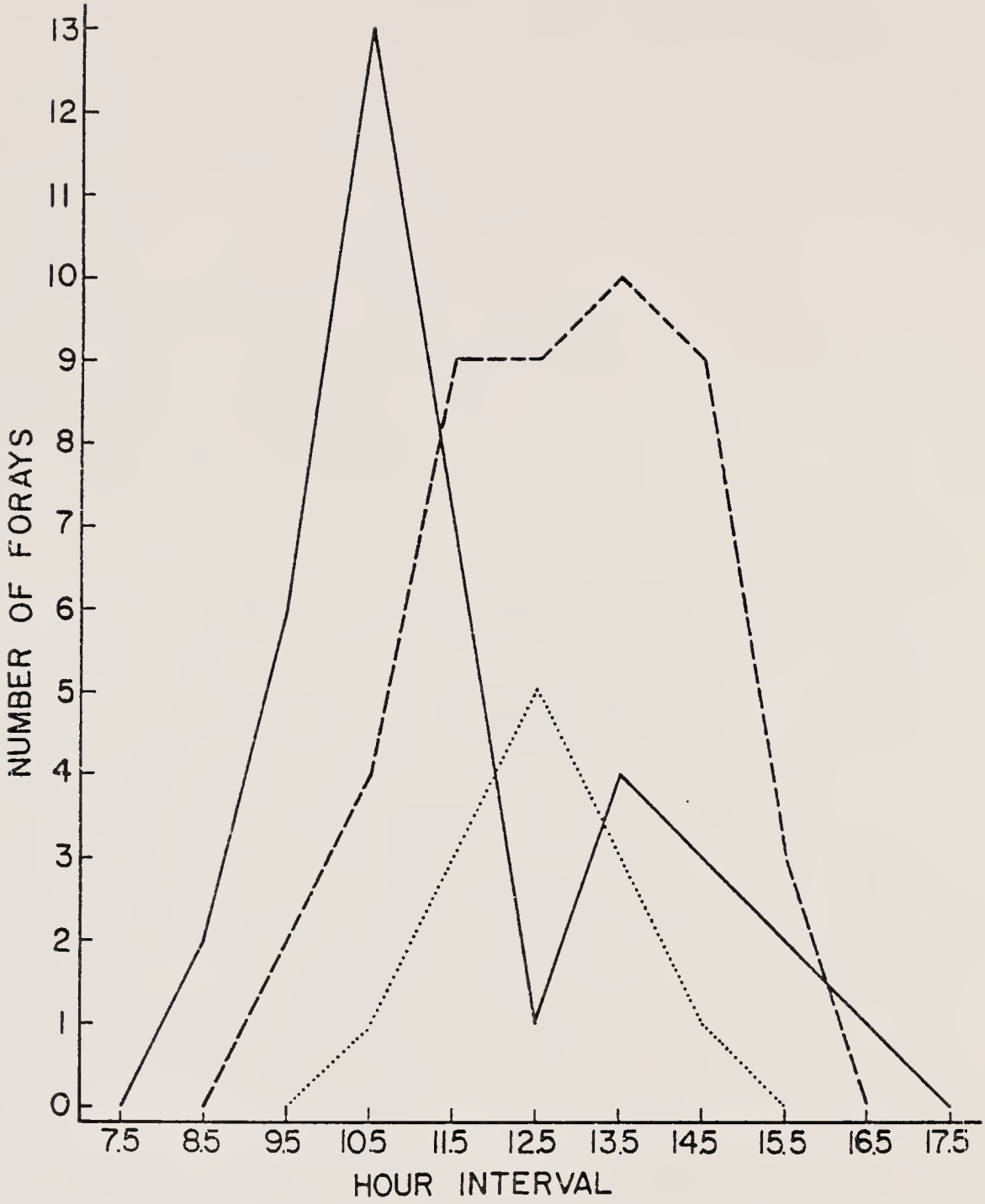


Figure 51. Daily change in the pattern of travel during forays. Results are illustrated for two lizards tracked for a total of 17 days in February plus October. Lizards walked in either a circular or elliptical clockwise path (solid line), approximately linear path (dotted line), or counterclockwise circular or elliptical path (dashed line).

Table 19. Skin patch heating. Six patches of integument were removed from a single *Cyclura carinata* adult, dried, and heated repeatedly from 20 to 50 C (T_a = 20 C). The heat lamp was oriented normally to the patch or at one of five different, less than normal angles, both directly anterior and directly posterior to the imbricate edges of the scales.

	HEATLAMP ORIENTATION ANGLE (DEGREES FROM NORMAL)					
	0	15	30	45	60	75
	HEATING RATES (SECONDS/30 C)					
			1. VENTRAL ABDOMEN			
Normal	34.4					
Anterior (A)		33.8	39.3	57.1	116.4	411.1
Posterior (P)		36.9	42.6	59.7	130.9	391.2
A/P		0.92	0.93	0.96	0.89	1.05
			2. DORSAL DISTAL HINDLEG			
	27.2					
		36.9	45.1	52.0	145.1	490.8
		37.3	44.9	53.5	147.1	453.8
		0.99	1.00	0.97	0.99	1.08
			3. DORSAL ABDOMEN			
	31.3					
		32.1	36.0	57.3	143.3	398.6
		34.6	35.7	55.4	110.0	289.8
		0.93	1.01	1.03	1.30	1.38
			4. DORSAL DISTAL FORELEG			
	39.4					
		37.7	52.4	75.0	141.8	335.0
		38.0	45.9	66.4	123.6	240.2
		0.99	1.14	1.13	1.15	1.39
			5. DORSAL PROXIMAL TAIL			
	55.9					
		59.2	64.7	90.7	169.0	626.8
		52.6	59.6	68.2	120.0	303.8
		1.13	1.09	1.33	1.41	2.06
			6. VENTRAL PROXIMAL TAIL			
	42.7					
		48.1	50.5	85.8	217.0	780.5
		41.8	45.7	61.4	111.7	289.4
		1.15	1.11	1.40	1.94	2.70

Dipsosaurus and *Sceloporus*, which have dorsal trunk scales arranged in rows parallel to the long axis of the body, *Cyclura* scale rows run obliquely toward the mid-sagittal crest at an anterior angle of approximately 60°. The radiant source should be normal to the scale rows of the dorsal trunk to maximize heat input. Thus, a maximally heating iguana should orient its body obliquely away from the sun, at an angle approaching 120°. Basking iguanas observed in the field and pen, in both the morning heating and regulating T_b phases, commonly oriented at slightly more than 90° (Figure 50). However, the degree of difference from normality for the peak in the frequency distribution of perpendicular orientations was within the range of error for the technique used to determine the orientations. Unfortunately, the definitive test, repeated radiative heating of individual lizards at different orientation angles in a constant thermal environment, was performed on only one adult male iguana. The maximum heating rate did occur at 120° (T_b = 13 C, T_b range = 20-25 C, single heat lamp angled 35° below the horizontal, angles of incidence from 0 to 180° at 30° plane intervals). Sample size, however, was obviously too small to draw any conclusion.

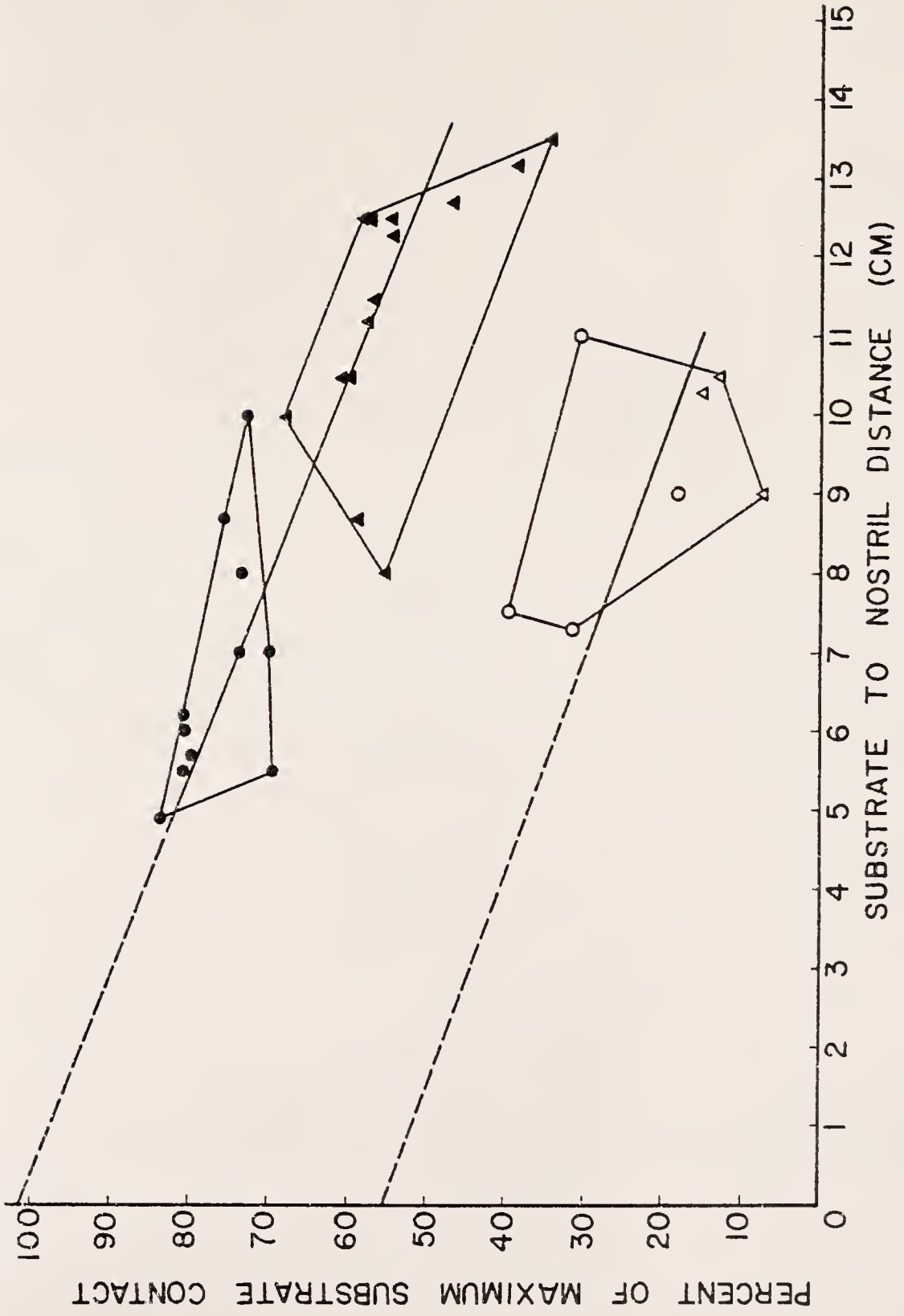
Thigmothermia

The relationship between surface area (cm^2) and body weight (g) in *Cyclura* was estimated by using a linear regression equation generated from Norris' data (1967) for eight species of iguanid lizards (Log Surface Area = 0.688 Log Body Weight + 1.025, N = 13, r = 0.996, $p \leq 0.0005$). The maximum possible substrate contact of an unanesthetized

lizard was assumed to be equal to the value for the same anesthetized lizard. Maximum substrate contact ranged from 13.4 to 16.0 percent ($\bar{X}$ = 14.3, N = 4 adults) of the total estimated surface area. Minimum substrate contact for a nonmotile lizard (Figure 44, Illustration 13), consisting of a small patch of distal tail and palmar plus plantar surfaces of the feet, averaged 1.1 percent of total estimated surface area. A lizard running across a hot substrate made even less instantaneous substrate contact.

When only the head and neck or only the head, neck, and forelegs were involved in substrate contact reduction, head elevation, as measured by the substrate to nostril distance, was linearly and inversely related to substrate contact (Figure 52). Lizards in the photothigmotron did not make substrate contact with the head, probably due to disturbances: intermittent moving of the camera as well as the noise and vibrations of the water bath. The upper regression line did extrapolate to approximately 100 percent contact at zero head elevation. Thus, maximum substrate contact must be about equal in anesthetized and unanesthetized lizards. A second regression line was fitted to the data for rear leg participation in substrate contact reduction. It had about the same slope as the upper regression line, as demanded by simple geometry. Reduction of substrate contact by elevation of only the posterior portion of the body was never observed. Maximum substrate contact must be energetically inexpensive, since the posture is a consequence of only the force of gravity on body tissues and muscular relaxation equivalent to an anesthetized state. Animals in this posture had slightly concave vertebral columns when viewed from the side. Buccal inspiration (gular pumping) was more common than in the more upright

Figure 52. Participation of the lizard's head, neck, and legs in the reduction of substrate contact. Data for a single adult female in the photothigmotron are illustrated. The lizard elevated only its head and neck off the substrate (solid circles), utilized its forelegs as well (solid triangles), or both its fore and hindlegs (open circles and triangles; some or no abdominal contact, respectively). The correlation coefficient for the linear regressions were -0.841 (upper line, $p \leq 0.0005$) and -0.432 (lower line, $p > 0.05$).


PERCENT OF MAXIMUM SUBSTRATE CONTACT
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
SUBSTRATE TO NOSTRIL DISTANCE (CM)

postures, probably due to the decreased efficiency of the thoracic inspiratory musculature.

Percent reductions in substrate contact by head-neck-trunk elevation and lateral compression were determined for three adult iguanas from their photothigmotron photographs. Lateral compression of the trunk was defined as the area difference between actual thoracic plus abdominal contact and the maximum possible contact for that area in the anesthetized lizard. Lateral compression's contribution only exceeded that of body elevation when the lizards were nearly completely relaxed on the substrate and never exceeded 16 percent of the maximum possible contact (Figure 53). Body elevation reductions of approximately 1-7 percent, due to changes in head contact, did not occur. Reductions of approximately 8-15 and 16-48 percent were due to head-neck and head-neck-foreleg participations, respectively. Trunk elevation instantaneously increased by 20-30 percent when the hindlegs came into action. The actual elevation increases were even larger since decreases simultaneously occurred in leg and tail contact. Complete lateral relaxation did not occur between trunk elevations of 16 and 37 percent; that is, over much of the range of the upright posture. Complete lateral relaxation of the hindtrunk vs. foreleg involvement in forebody elevation appear to be partially mutually exclusive.

Ventral body contact responses to *Cyclura* in different conductive-convective environments were usually thermoregulatorily adaptive (Figure 54). The lizard made greater ventral contact while heating in positive $T_s - T_a$, $T_s - T_b$ environments (Experiments I - III) than when cooling in negative $T_s - T_a$, $T_s - T_b$ environments (Experiments IV, V), with a maximum heating-cooling contact range of 38 percent. Note how contact declined

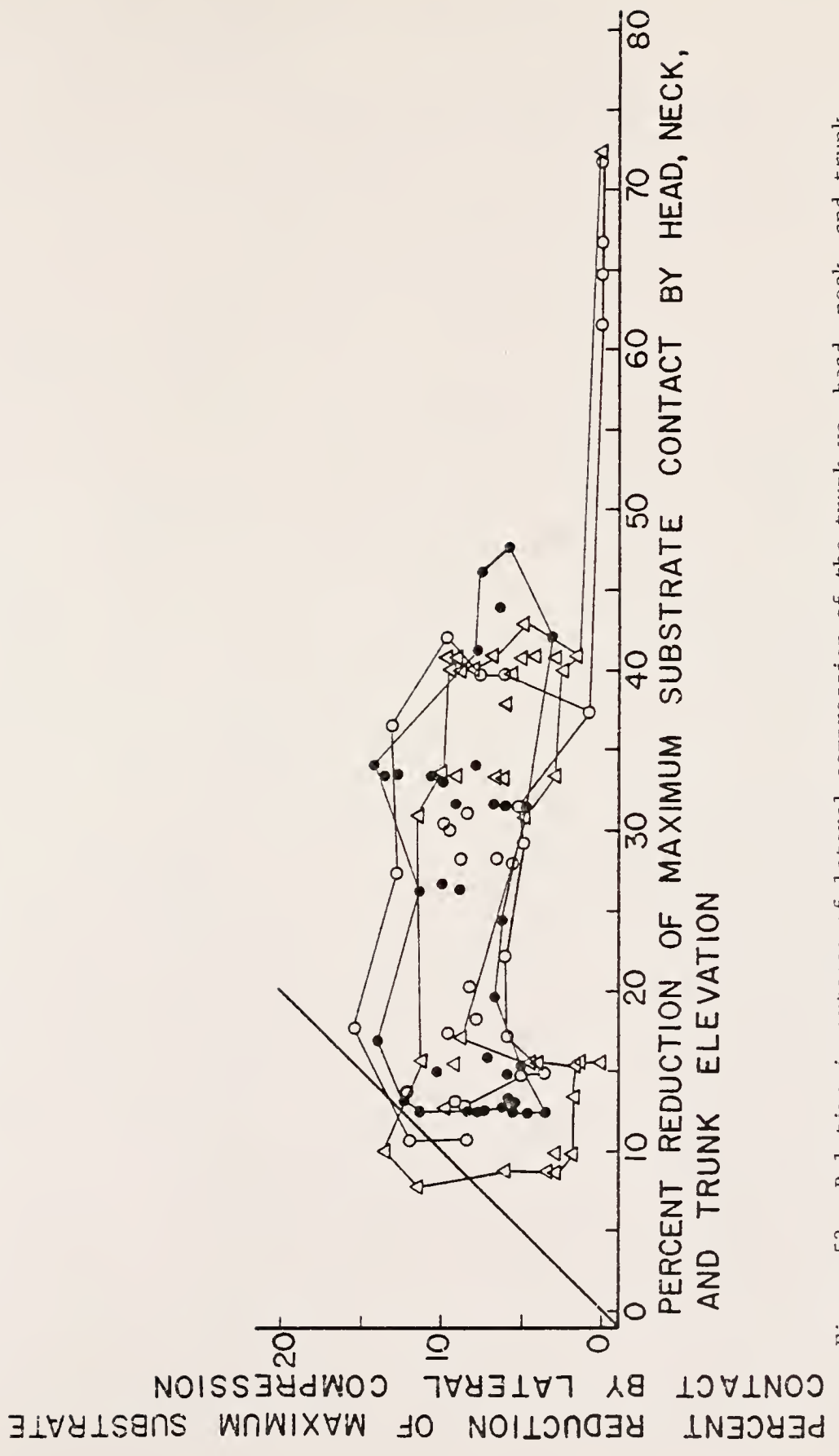


Figure 53. Relative importance of lateral compression of the trunk vs. head, neck, and trunk elevation in reducing substrate contact. Three lizards, represented by solid circles, open circles, and open triangles, were each monitored in the photothigmotron for several days under differing environmental conditions.

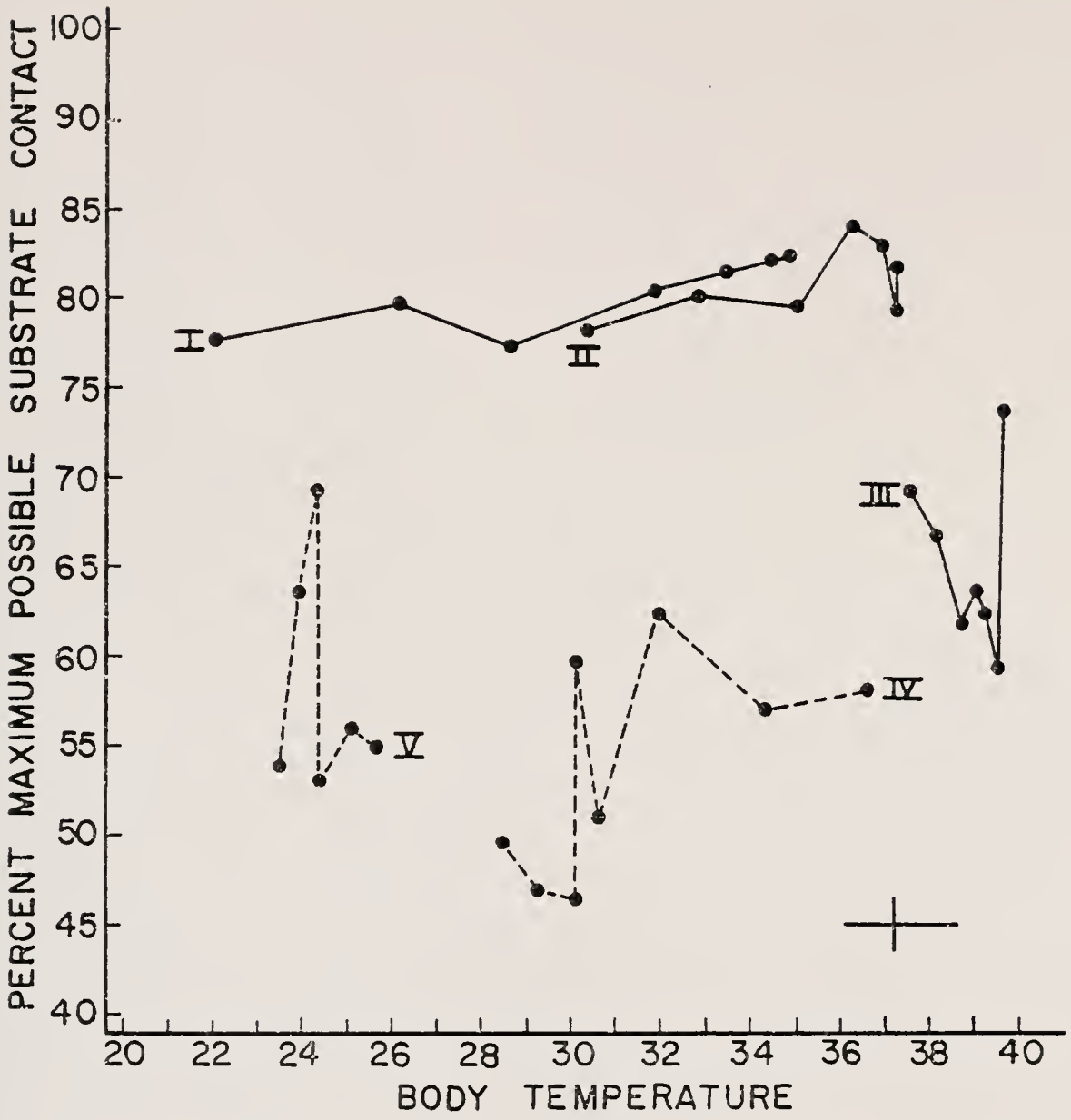
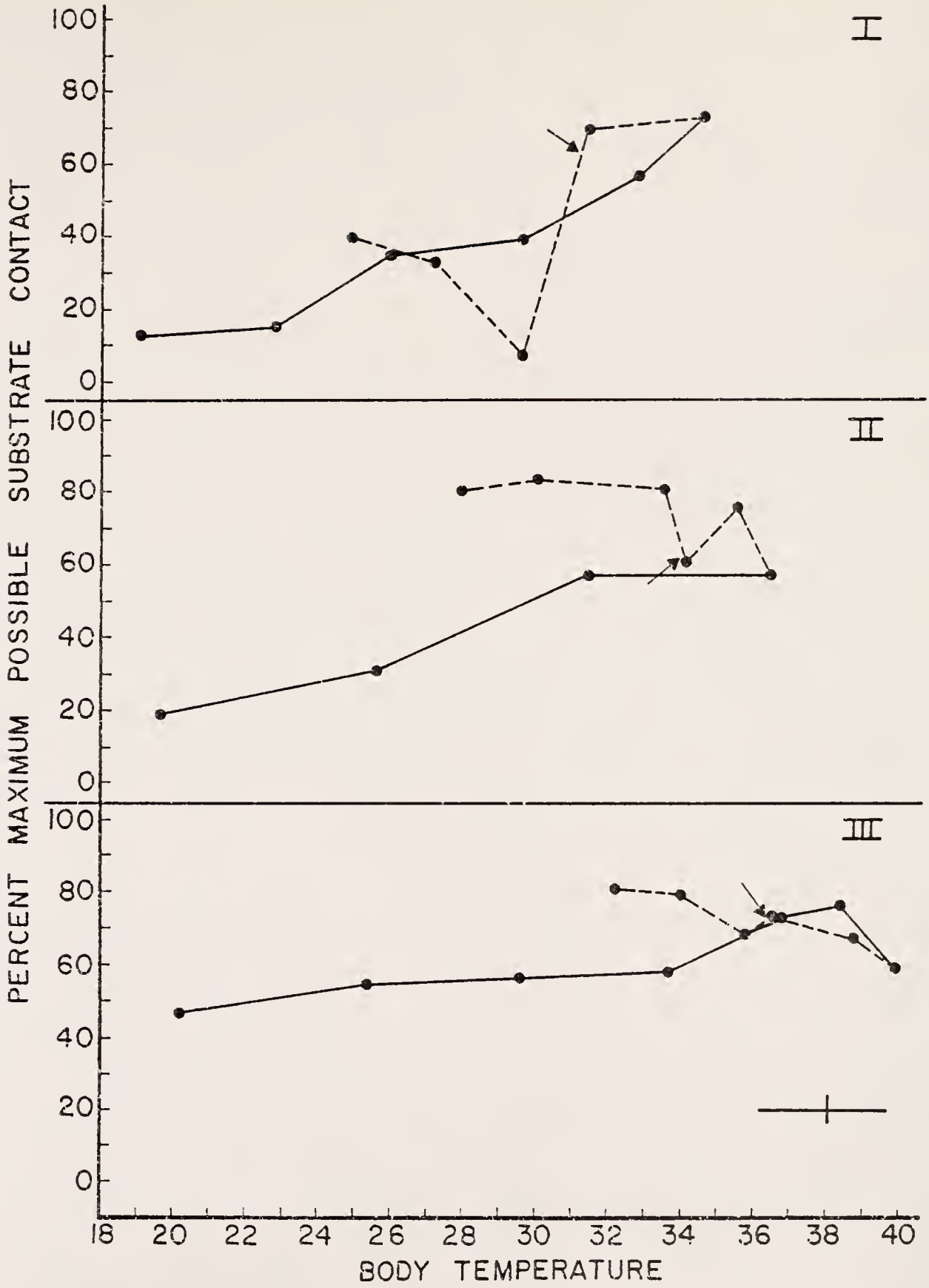


Figure 54. Conductive and convective heating and cooling of a single *Cyclura carinata*. Experiments were run on five consecutive days for a 1135 g adult female: I; T_a = 23 C, T_s = 41, II; T_a = 29; T_s = 41; III; T_a = 36, T_s = 41, IV; T_a = 38, T_s = 21, V; T_a = 27, T_s = 19. The lizard was either heating (solid line) or cooling (dashed line). Maximum substrate contact was assumed to be equivalent to that of an anesthetized state. The lizard's mean regulating phase T_b and range in the thermal gradient are indicated by the vertical and horizontal lines, respectively.

in III as T_b increased to above the preferred range. The lizard was probably attempting to decrease conductive heat input as well as cool itself convectively. As T_b asymptotically levelled at the end of run III, the lizard relaxed somewhat on the substrate. The lizard did not immediately minimize substrate contact in IV as expected, but rather gradually reduced it as burrow T_b was approached. The technique utilized to start the run, that is, pulling out the insulating plywood substrate, inevitably startled the animal. Immediate minimization of contact may have been learned had each experiment been repeated several times. Also, the high T_b at the beginning of the run may have partially overridden the peripheral heat receptor inputs. The lizard responded with the appropriate thermoregulatory posture to fairly small $T_s - T_a$ differences (5 C in III, -8C in V). The upright posture was still maintained at the end of V even though T_b was only 4.5 C above T_s and 3.5 C below T_a. Significant differences in substrate contact at equal gut temperatures, as in I vs. V and II vs. IV, were probably primarily due to differences in peripheral temperature receptor inputs to the brain. This was especially true in I vs. V, where brain-gut temperature differences were small due to the nearly equal T_a's in the two experiments (23 and 27 C).

Figure 55 illustrates some of the ways *Cyclura* responded to simultaneous radiant heating and conductive heating or cooling. Substrate contact increased as T_b increased in all three experiments, as was observed during the morning heating phase in the field. Substrate contact at low T_b was greatest in III, the run with the highest substrate temperature. However, the lizard did not maximally flatten in III at low

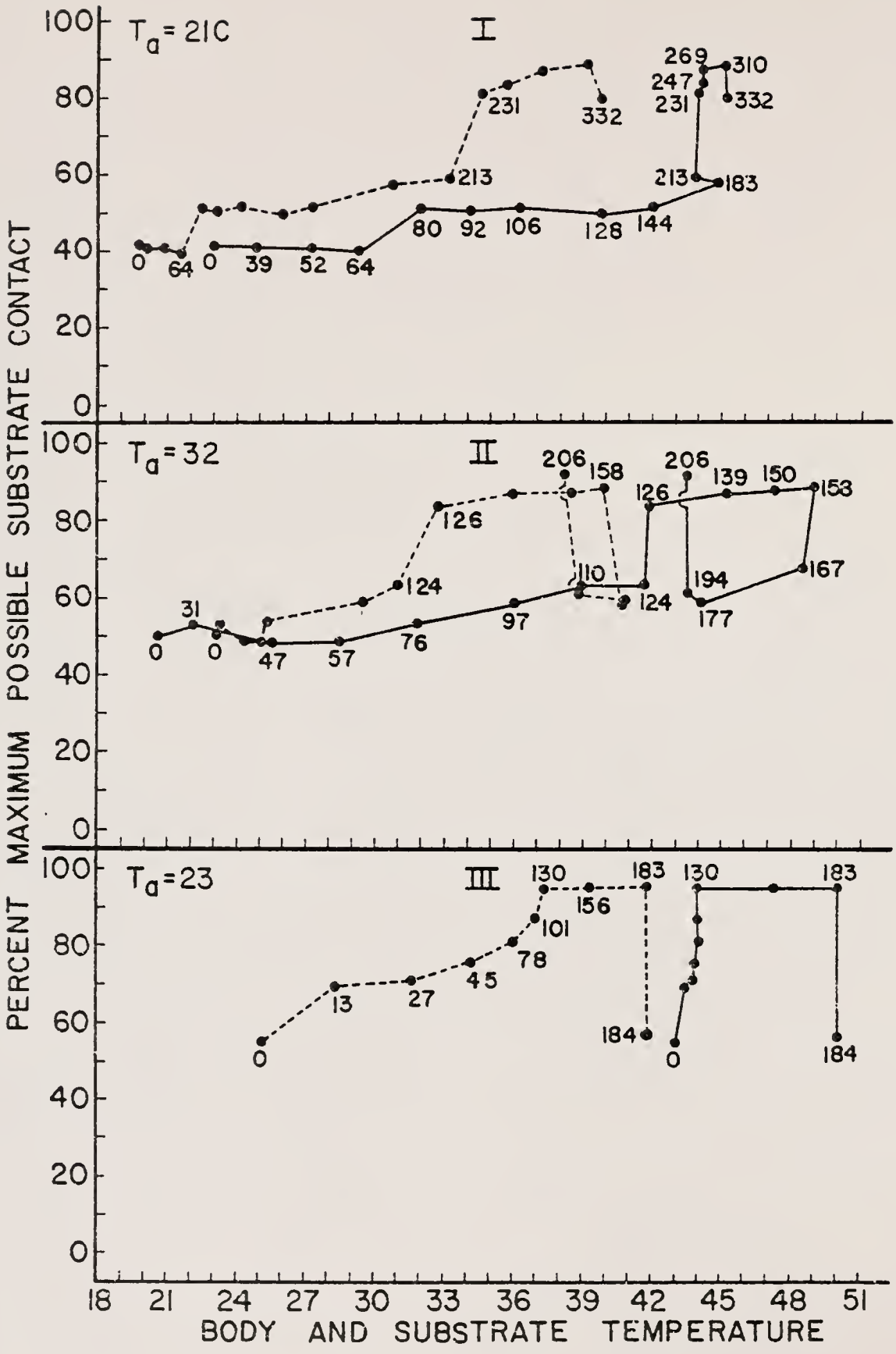
Figure 55. Conductive heating and cooling of a single *Cyclura carinata*, with and without simultaneous radiative heating with a heat lamp. Experiments were run at a constant air temperature (19 C) on three consecutive days for a 985 g adult female; I; T_S = 20 C, II; T_S = 31, III; T_S = 38. The lizard was either heating (solid line) or cooling (dashed lines). The heat lamp was turned off at the points marked by the arrows. The lizard's mean regulating phase T_b and range in the thermal gradient are indicated by the vertical and horizontal lines, respectively.


I
II
III
100
80
60
40
20
0
PERCENT MAXIMUM POSSIBLE SUBSTRATE CONTACT
18
20
22
24
26
28
30
32
34
36
38
40
BODY TEMPERATURE

T_b. Rather, it balanced heat intake from conductive and radiant sources. Further increases in substrate contact would have decreased radiant input, due to the considerable angle of the heat lamp. As T_b increased from I to III, the lizard reached increasingly higher T_b's before moving away from the heat lamp. Core temperature at radiant heat escape rose 5.3 C, from 34.6 to 39.9 C, while substrate temperature increased 18 C, from 20 to 38 C. Thus, the T_b - T_s difference decreased from 14.6 to only 1.9 C! The lizard was probably regulating skin surface temperature rather than gut temperature. When surface temperature reached a narrow escape range, the iguana departed, at a low T_{gut} on cold substrate, at a higher T_{gut} on warmer substrates. When the heat lamp was turned off in I, the lizard soon reduced contact nearly maximally due to the low T_s. However, maximum elevation was only briefly maintained. The posture, utilizing both fore and hindlegs in a walking stance, was probably too strenuous to maintain for long periods. The lizard cooling in II reached nearly maximum substrate contact at a T_b of 2.5 C above T_s. The substrate was still a heat sink. This demonstrates the mistake of assuming thigmothermia just because the animal relaxes on the substrate. Maximum contact was a response to low T_a and the small T_b - T_s difference. In the field, the conductive heat loss while maintaining a maximally prostrate posture on a substrate slightly cooler than the body core may be less than the forced convective heat loss if the animal assumed an upright posture.

Figure 56 illustrates the changes in substrate contact of a lizard subjected to increasing, stable, and decreasing substrate temperatures, with T_a held constant and no radiant heating with a heat lamp. Substrate contact increased as T_b increased, as in Figures 54 and 55.

Figure 56. Thigmothermic responses of a single *Cyclura carinata* to periods of increasing, stable, and decreasing substrate temperature. Experiments were run on three consecutive days on an adult male weighing 1288 g. Body and substrate temperatures vs. percent substrate contact have been plotted (dashed and solid lines, respectively). Minutes since t_o, the start of the experiment, are indicated by Arabic numbers. The lizard was in thermal equilibrium with air and aluminum substrate temperatures at T_o of Experiments I and II and with T_a and the cool plywood substrate temperature at T_o in Experiment III, at which time the plywood was removed.


PERCENT MAXIMUM POSSIBLE SUBSTRATE CONTACT
BODY AND SUBSTRATE TEMPERATURE
T_a = 21C
I
T_a = 32
II
T_a = 23
III
0
20
40
60
80
100
18
21
24
27
30
33
36
39
42
45
48
51

The greatest rate of increase of substrate contact occurred at T_b ranges of 33.3-34.6 (I), 31.0-32.7 (II), and 36.0-37.4 C (III) (T_s - T_b = 9.4-10.5, 7.9-9.8, and 6.7-9.7 C, respectively). Smaller T_s - T_b's were coupled with lesser substrate contacts. Due to the low T_a, the lizard relaxed nearly maximally at a T_s as high as 50.1 C in III, a T_s approximately 3.9 C above the mean critical thermal maximum of the body core. Substrate contact was abruptly reduced when T_b moved into the upper voluntary tolerance range. A contact cycle was produced in II by first increasing, then decreasing substrate temperature.

Low Body Temperature Behavior

Behavioral responses were lost during cooling in order of decreasing energy demand and neural pathway complexity, and regained in the reverse order during heating, at approximately the same intestinal temperatures as during cooling (Figure 57). Crawling, the most energetically demanding behavior, was lost first, and opening the eyes, the least demanding, was lost last. Running and walking abilities were lost sequentially at higher T_b's, but the actual temperatures were not determined. Bloating was the next to the last response lost before lizards became completely immobilized. Lizards utilized the hyoid musculature to maximally inflate the lungs, greatly increasing the circumference of the trunk. Thus, a nearly helpless animal could still wedge itself securely in its burrow or, perhaps, intimidate a predator by bloating.

Lizard critical thermal minima (Spellerberg 1972a) and maxima (Lowe and Vance 1955, Larson 1961) increase, within limits, as acclimation temperature increases. The mean critical thermal minimum

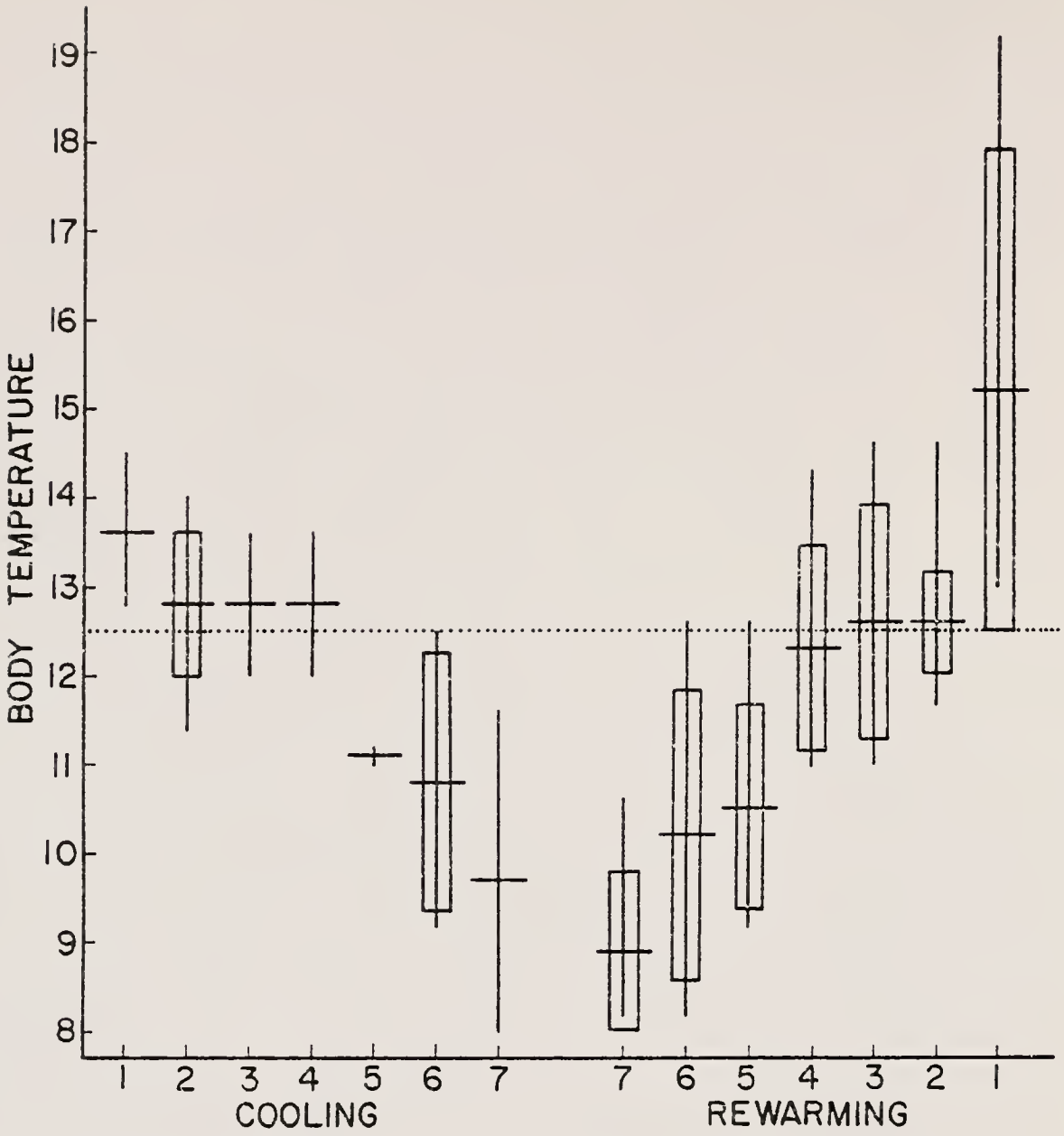


Figure 57. Behavioral responses of *Cyclura carinata* at low body temperatures. The temperature of the large intestine was recorded when a lizard lost and regained each of seven behavioral responses during cooling and reheating, respectively: 1. crawling, 2. turning over when placed on the back (critical thermal minimum), 3. maintaining the head in a horizontal orientation with respect to the ground when the body long axis was elevated and depressed at the tail, 4. maintaining a constant field of view by rotating the head or eyes when the body was rotated laterally, 5. moving the legs when pinched while placed on the back, 6. bloating, 7. closing and opening the eyes. The sample contained six adults. Horizontal lines are means, vertical lines; ranges, and rectangles; plus and minus two standard errors of the mean. The dotted line marks the lowest temperature recorded during the study (exposed substrate temperature; Iverson 1977).

for summer lizards in the Caicos was probably one to two degrees higher than 12.8 C, which was calculated for animals acclimatized to late May environmental temperatures in Gainesville. In support of this hypothesis, all lizards acclimatized to the Caicos summer were completely anesthetized at 10 C when cooled for transmitter implantation.

A lizard must meet several locomotory requirements, one of which is to move successfully from place to place at the lowest T_b it is ever likely to endure. It isn't surprising, then, that *Cyclura*'s CTMin was well correlated with the lowest environmental temperature recorded during the study, 12.5 C. The correlation holds for other lizards examined thus far (Spellerberg 1972b). *Cyclura* probably experienced a T_b of 12.5 C on only rare occasions, unless sequestered for the night in a surface level retreat, since cold fronts did not last long enough for deep soil temperatures to fall this low.

The CTMin varies significantly for lizards living at different latitudes. *Liolaemus multiformis*, ranging high into the Andes of southern Peru, is able to move about slowly at a T_b of 1.5 C (Pearson 1954). The 29 species of lizards from southeastern Australia examined by Spellerberg (1972a) all had CTMin's lower than *Cyclura*'s. Expectedly, minimum environmental temperatures fell lower there than in the Caicos. Both *Anolis carolinensis* and *Sceloporus occidentalis* have similar CTMin's to *Cyclura*'s (Kour and Hutchison 1970).

The CTMin of some lizards could be lowered by acclimation to below -0.52 C, the freezing point of the whole body (Spellerberg 1972a). That is, the lizards could still turn over when supercooled. This probably would not be true for *Cyclura*, since none of Spellerberg's acclimation ranges approached the necessary 13 C. The acclimation

range appears to be greater for the CTMin than for the CTMax (Kour and Hutchison 1970). This is logical since lizards can always retreat from high environmental temperatures, but not from minimums passively experienced while in a nocturnal retreat. The correlate of this is Spellerberg's finding (1972a) that the CTMin was better correlated than the CTMax with the geographic distribution of lizards.

When placed on its back, held firmly for a few seconds with legs adpressed to the trunk and tail, and then gently released, *Cyclura* remained quiescent for short periods before righting itself. This so-called tonic immobility has been induced in other lizard species (Prestrude and Crawford 1970, Hennig and Dunlap 1978). The righting response could be induced prematurely by gentle poking of the body. On the contrary, it could not be induced, even by strong prodding, once the lizard had reached the CTMax or CTMin. Thus, tonic immobility did not obscure the CTM determinations.

The lethal minimum body temperature was not determined. However, two summer acclimatized lizards cooled to 0 C in the Caicos were partially paralyzed and subsequently died after rewarming.

High Body Temperature Behavior

Panting in *Cyclura* was a proportionally controlled behavior, probably with various effector outputs directly proportional to the sum of positive deviations of many body temperatures from a reference set-point temperature, presumably located in the hypothalamus. Effector outputs consisted of the gaping time per minute, the degree of gape, the extent of elevation and blood engourgement of the tongue, and probably, the respiratory and salivation rates. The panting threshold temperature,

at which the lizard initially gaped, was estimated by gut and head temperatures. Unfortunately, the respiratory rate was not determined during gaping of restrained lizards heated in the field. It is probable, however, that the respiratory rate increased as T_b rose during gaping. Thus, *Cyclura* is a true panting lizard rather than a thermal gaper, a lizard with reduced ventilation rate during gaping (Heatwole *et al.* 1973).

Radiantly heated, restrained lizards in the field initially panted for only a few seconds. As T_b continued to rise, tongue elevation and the degree of gaping increased and the mouth was closed less often, eventually only long enough to recoat the surface of the tongue and walls of the buccal cavity with saliva (Figure 44, Illustrations 13 and 14). The saliva secretion rate appeared to increase with T_b. Well hydrated lizards, fed white grapes in the Gainesville pen, salivated sufficiently to overflow the mouth and form a droplet on the lower jaw. On the other hand, three lizards heated in the field in June did not drool at all, probably due to the lower water content of their food. Restrained lizards alternated between panting bouts and struggling to free themselves from their tethers. Panting ceased during struggling. It could also be stopped briefly by scaring the animal.

The mean intestinal heating rate in three restrained, morning sun heated lizards dropped from 0.111 C/min just before panting commenced to 0.069 C/min during panting, even though heat input was increasing with time. It is likely that the reduction in head heating rate was even greater (Crawford 1972).

Eye bulging, which usually became visually apparent soon after or before panting commenced and continued at least until the CTM was reached, gave the lizard a perpetual stare. It probably resulted from contraction of the jugularis muscle surrounding each internal jugular vein, increasing the blood pressure in the orbital venous sinuses between and around the eyes and diverting venous flow to the external jugular and vertebral veins (Heath 1966). Eye bulging probably serves the same two functions it does in *Phrynosoma*. The skin immediately around the eyes was commonly the first head skin shed during the single annual molt in *Cyclura*. Eye bulging may aid in this process. During two successive heating runs of a single large male in the photothigmotron, the head heating rate decreased very soon after eye bulging and considerably before panting commenced. Head temperature was 3.4 and 3.9 C above gut temperature. Head heating decreased from 0.59 and 0.40 C/min to 0.09 and 0.07 C/min, respectively, a mean reduction of 84 percent. Gut temperature continued to rise steadily after bulging in the first run, at a rate of 0.10 C/min. However, in the second run, it increased from 0.04 to 0.08 C/min, as expected if the body core was functioning as a heat sink for the head. Thus, rerouting venous blood away from the internal jugular vein-internal carotid artery countercurrent heat exchangers during eye bulging probably lowers the positive T_{head}-T_{body} difference at high temperature. Eye bulging may serve a head cooling function both in emergency in conjunction with panting and alone in less urgent situations below the panting threshold T_b.

The gut temperature range for the panting threshold was at least 11.0 C, from 32.8 C for a jig restrained lizard during heating in the

controlled temperature room in August, to greater than 43.8 C, the T_b maximum for free-ranging lizards basking without panting in the late afternoon. The threshold declined as heat input increased at midday and again increased in the afternoon as heat input waned (Figure 58). This is further evidence for a peripheral heat receptor input influencing an effector output.

The log of the total panting time after shading in the roof top arena was well correlated with the sum of the gut and head temperature lag times, and less well correlated with each separate time (Figure 59). The multiple linear regression was: Log Total Panting Time = -1.421 + 0.097 Gut Lag Time + 0.115 Head Lag Time. Thus, gut and head temperatures appear to be about equally important in determining the total panting time after shading. As the sum of the gut and head temperature lag times increased linearly, the panting time increased exponentially. The reason for this was that the longest panting times occurred during the hottest part of the day, when the highest shaded air and substrate temperatures occurred, as well as the greatest radiant input from the aluminum walls of the arena. Although head temperature fell rather rapidly after shading and panting commenced, gut and body surface temperatures did not.

The intestinal temperature at the critical thermal maximum averaged 46.2 C (46.0-46.3) for three freshly caught *Cyclura* heated in the sun starting at 0700 on July 2 (body weights = 150, 536, and 800 g). The head-intestine temperature difference was probably +1-2 C at the CTM, even though the mean intestinal heating rate after panting commenced was only 0.07 C/min. In the turtle *Chelodina longicollis*, the head-body temperature difference at the CTM increased with body weight, from

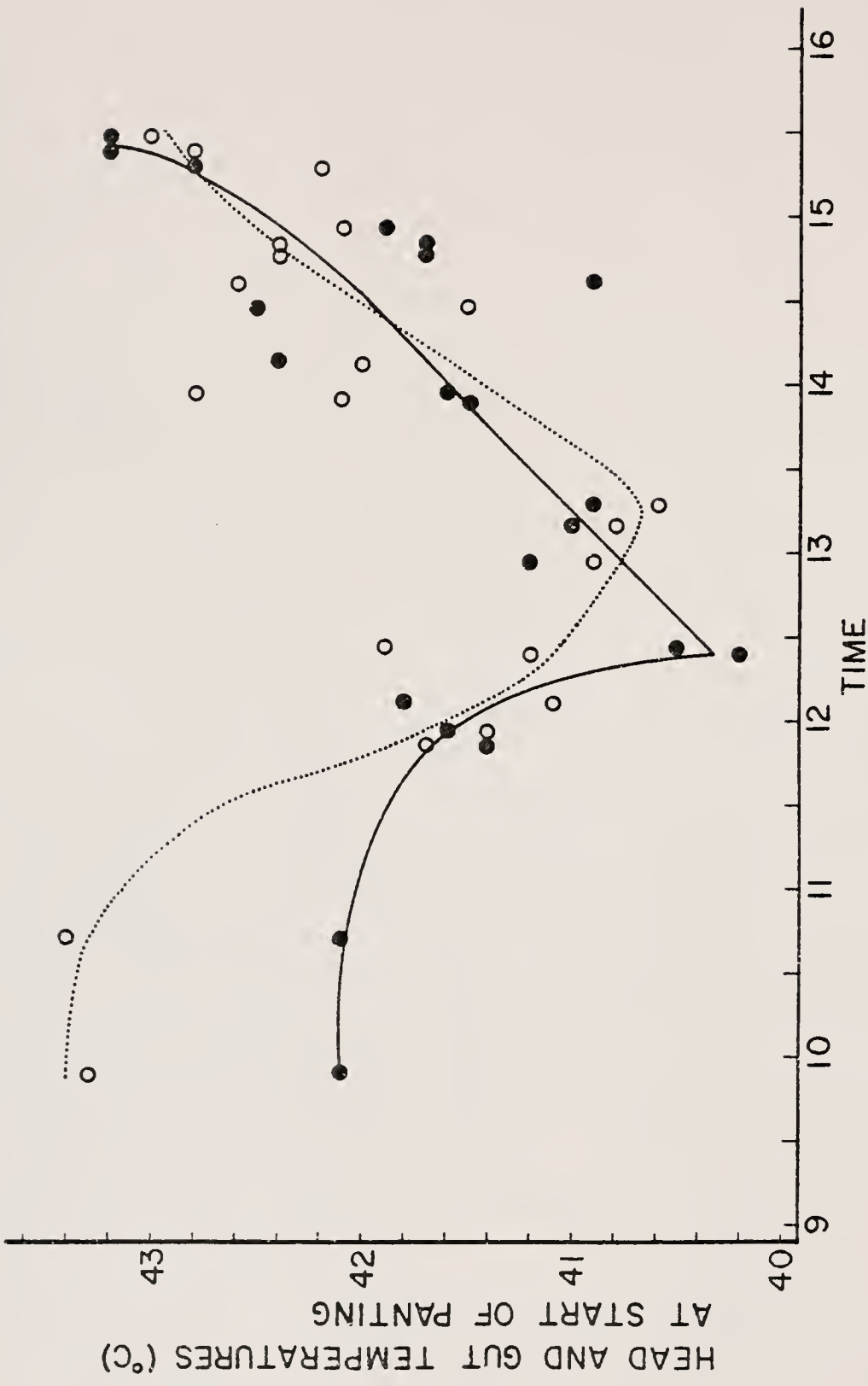
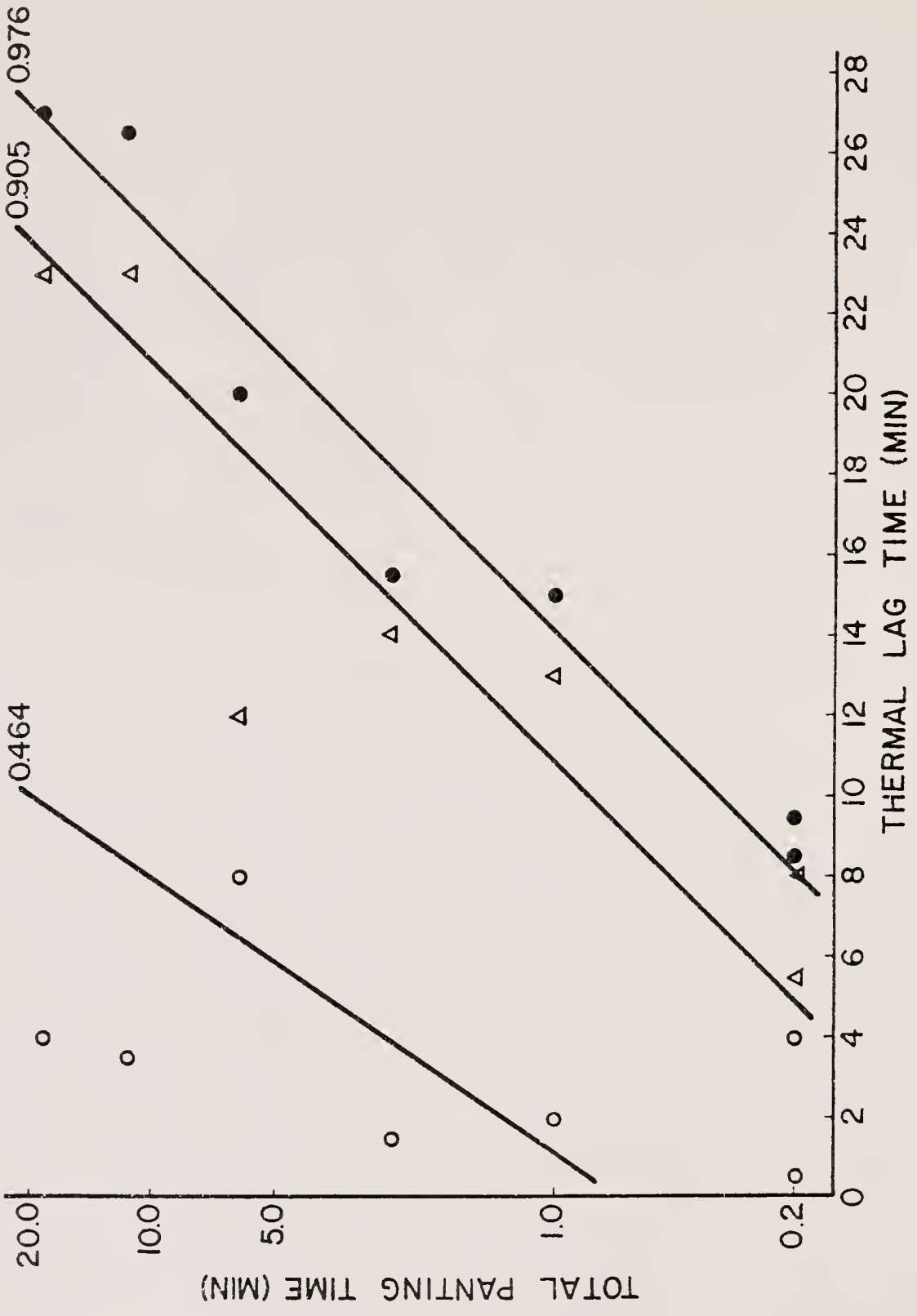


Figure 58. Daily adjustment of the panting setpoint to changing heat input. A 1790 g male was repeatedly heated to the panting setpoint (gut temperature; solid circles and line, middle ear temperature; open circles and dotted line) while contained for two days in July in a rooftop arena in Gainesville. Curves were fitted by eye.

Figure 59. Correlation of total panting time with head and gut thermal lag times. A single 1790 g male was repeatedly heated to panting during two days in the rooftop arena and immediately shaded when panting commenced. The length of time that head temperature (open circles), gut temperature (open triangles), and the sum of both (solid circles) continued to rise after shading (lag times) have been plotted against the total minutes of each panting bout. The correlation coefficients for the three linear regressions are indicated at the top of each line.


0.976
0.905
0.464
20.0
10.0
5.0
1.0
0.2
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
TOTAL PANTING TIME (MIN)
THERMAL LAG TIME (MIN)

approximately 0.8 C at 100 g to 3.5 C at 1200 g (Webb and Witten 1973). The head temperature at the CTM was independent of body weight, but the posterior body temperature at the CTM decreased with increasing body weight. Thus, head temperature as well as gut temperature should have been measured during CTM determination in *Cyclura*.

When both panting and struggling ceased at 48.0 C (47.9-48.1), two lizards were rapidly cooled. Since neither recovered, 48.0 or lower must equal the lethal maximum (LM). The three lizards simultaneously reached the LM at 1025, even though body weights varied by a factor of five.

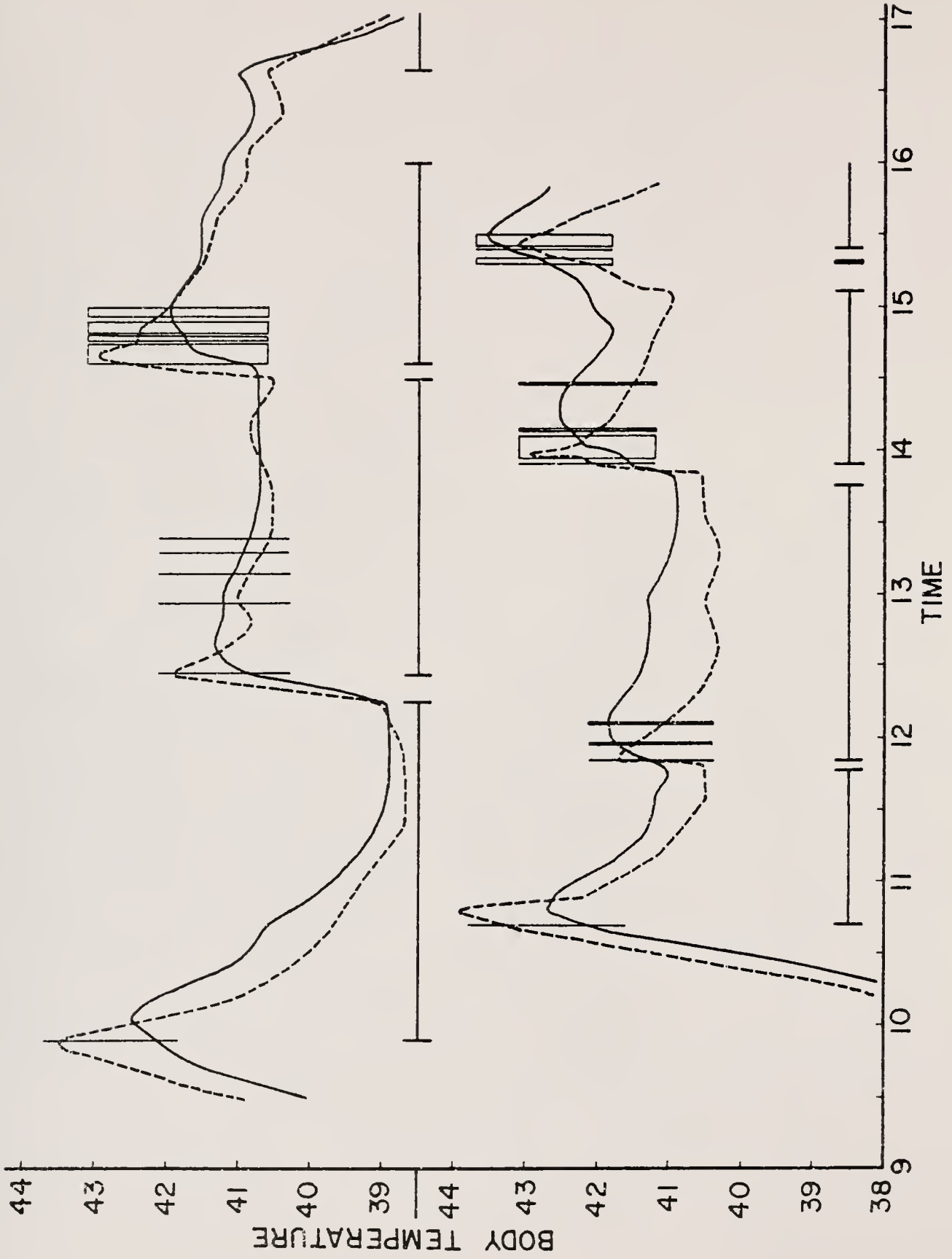
The minimum thermal safety margin (Heatwole 1970), defined as the difference between the maximum voluntary tolerance and the CTM, approximated 4.8 C at midmorning ($\bar{X}$ MVT = 41.4 C between 1000 and 1100 for eight hyperthermic summer lizards). The three lizards used in the CTM determination passed through the MTSM in a mean time of 68 minutes, sufficient to avoid fatal overheating during practically any high T_b encounter. Of course, the MTSM time decreased considerably as midday approached. For example, a 375 g male took only 15 minutes to heat from 41.4 C to its gut measured CTM of 44.9 C at 1310 on July 3. This value is low in comparison to the three lizards measured on July 2, probably due to an increased thermal lag between head and body temperatures as heating rate increased, rather than a lowering of the CTM as measured by head temperature. In fact, the CTM peaked around midday in two turtle species, *Chrysemys picta* (Kosh and Hutchison 1968) and *Chelodina longicollis* (Webb and Witten 1973).

Head-Body Temperature Differences

Gut and orbital venous sinus temperatures were monitored in a single 1600 g male *Cyclura* in the photothigmotron. Head-body temperature differences of up to +13.7 C were recorded (T_{air} = 40 C, $T_{substrate}$ = 20, heat lamp 30 cm from the lizard's head). The maximum head-body temperature difference was only -2.3 C when T_a and T_s were reversed and the heat lamp was directed at the lizard's trunk. The 11.4 C difference in the absolute values was primarily due to the greater surface to mass ratio of the head. In still air, T_s is more important than T_a in control of both head and body temperatures. For example, with a T_a of 21 C and a T_s of 40 C, the steady state head and gut temperatures were 32.6 and 34.7 C, respectively, 4.2 and 8.4 C closer to substrate than air temperatures. Lizards basking after a long burrow submergence on cool, rain soaked sand in the midday sun should have the largest transient head-body temperature differences. Individuals resting in the midafternoon shade, characterized by nearly stable gut and head temperatures and a small $T_s - T_a$, should have the smallest head-body temperature differences.

The head and body temperatures of a single iguana were monitored for two days in the Gainesville rooftop arena (Figure 60). When the lizard was in the sun, the head always heated faster than the gut ($\bar{X}$ head/gut heating rate ratio = 2.4, range = 0.9-6.0, N = 7) and head temperature usually exceeded gut temperature ($\bar{X}$ head-gut temperature = 1.0 C, range = -0.1-1.6 C). Thus, daily head temperature maxima for free-ranging lizards were probably higher than the coelomic and gut maxima listed in Table 1. In the shade, the lizard's head consistently

Figure 60. Head-body temperature differences during heating and cooling of a 1790 g male *Cyclura carinata* in the Gainesville rooftop arena. Head temperature was measured just inside the tympanum with the probe of a near-field transmitter (dashed line). Core temperature was measured in the gut with another near-field transmitter (solid line). The lizard was manually shaded (horizontal lines) immediately after panting commenced (vertical lines and rectangles).


BODY TEMPERATURE
44
43
42
41
40
39
38
9
10
11
12
13
14
15
16
17
TIME

cooled faster than its gut. The mean head-gut difference was -0.3 C (-1.5-0.4). It appears that the head-body temperature difference is greater during the heating phase than during the cooling phase. Head and body temperatures approached equality as the time in the shade increased.

The Integument: Metachromatism and Reflectivity

Head, trunk, and leg integuments were dark gray to charcoal black at low body temperatures during nocturnal inactivity, the first minutes of the morning basking phase, and long periods of overcast. Iguanas were usually darkest immediately after emergence. The ventral pectoral region was usually the darkest area on a lizard in its dark phase (Figure 61, #7). The proximal ventral tail was always the most highly reflective area (#4). Dorsal dark phase reflectivity was well matched to the fused coralline sand substrate, which was darkened by a thin encrustation of two species of blue-green algae (#2 vs. #3). Extensive tracts of this sparsely vegetated substrate lay along the windward side of Pine and Water Cays, interspersed with patches of cream colored dunes sand. Low lying karst ridges, as in Rocky Coppice, were also encrusted with the same algal growth. However, it was not determined whether lizards in their dark phase preferentially basked on dark substrates. The high *Cyclura* density associated with karst ridges in Rocky Coppice may be due in part to the advantages of dark hillsides to basking lizards: 1. good color matching at low T_b's, 2. fairly large unvegetated areas, 3. protection from the wind, and 4. high net heat input on sun-facing slopes. The greater abundance of burrows and greater diversity

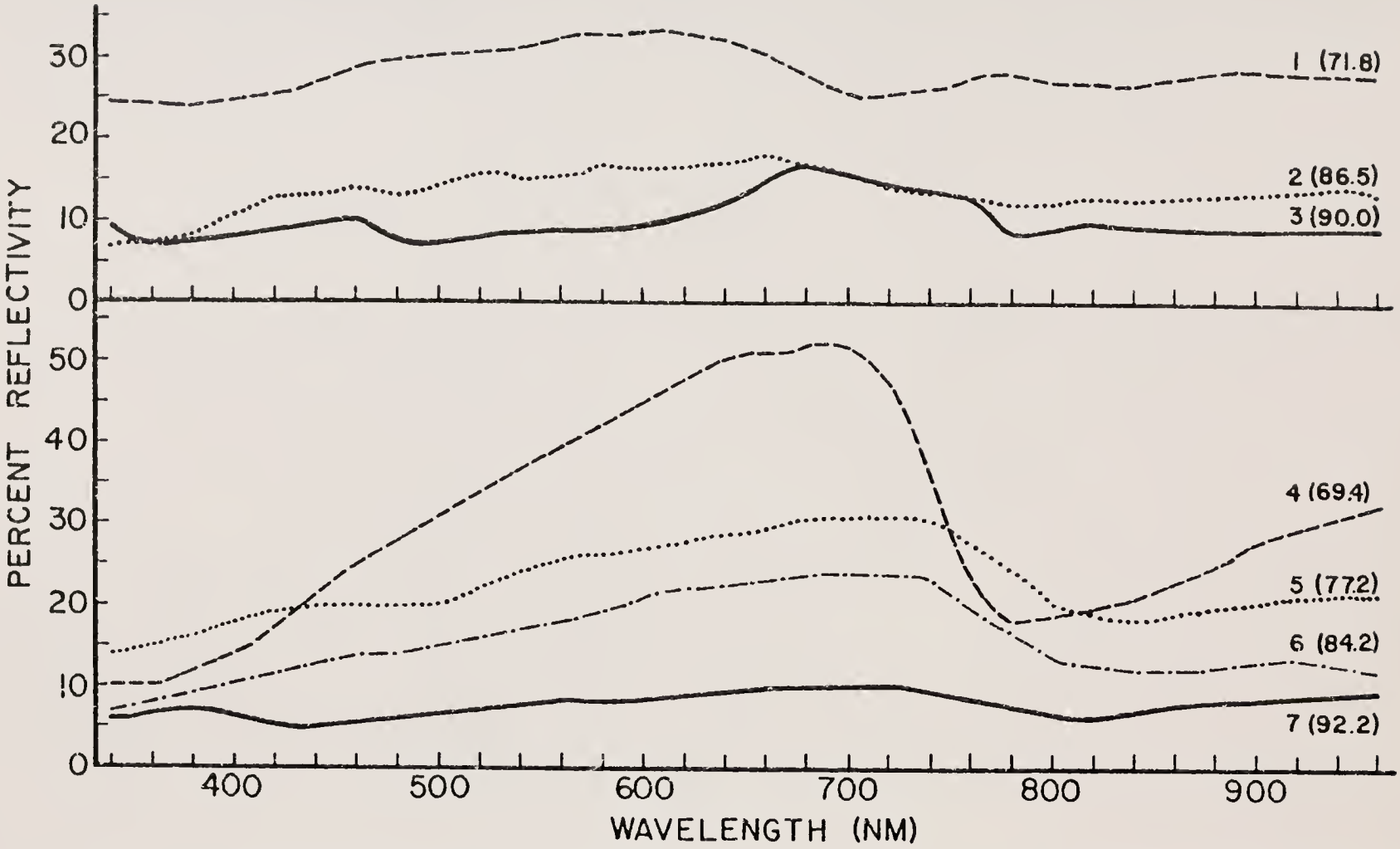


Figure 61. Integumental and substrate reflectivities. Skin patch 1 was excised from an adult Water Cay lizard in its light phase, patches 2, 4, 5, 6, and 7 from another Water Cay adult in its dark phase. Patches were excised from the 1) dorsal abdomen, 2) dorsal abdomen, 4) ventral tail immediately posterior to the anus, 5) ventral abdomen, 6) dorsal tail immediately posterior to the anus, and 7) ventral pectoral region. Reflectivity curve 3) is for a piece of a common Caicos substrate, fused coralline sand encrusted with two species of algae (Phylum *Cyanophyta*). Numbers in parentheses are mean percent absorbances.

of food plants in Rocky Coppice (Auffenberg in prep.) may also account in part for the high lizard density.

Live adult iguanas primarily absorbed rather than reflected near infrared light, as indicated by photographing them with Kodak Infrared Ektachrome film. The animals, appearing blue colored while in the regulating phase T_b range, stood out clearly from the surrounding red colored photosynthetic vegetation, which reflected near infrared light.

Lizards were well concealed in the scrub due to excellent color matching, countershading, and cryptic behavior. The integument lightened as body temperatures increased, a change well correlated with the animal's movement into the brush during the first foray. To varying degrees, the head, trunk and legs became pale yellow-green and light gray on Water Cay (Figure 61, #1) and Pine Cay lizards, respectively. Tail color change with increasing T_b was slight. Countershading made it difficult to distinguish the ventrolateral side of the lizard from the sand substrate. The ventral abdomen was grayish cream in the dark phase and cream colored in the light phase and was reflectively less labile than the ventral pectoral region and the dorsal body surface. Cryptic behavior enhanced concealment of lizards in the bush. The animal sat motionless in an upright posture until an approaching potential predator, in this case myself, was seen. The lizard soon walked about five to ten meters out of sight and sat motionless again. The behavior was repeated when I followed. On the contrary, when not habituated to humans, located in open areas, or recently emerged, lizards commonly ran to the nearest burrow without making any initial eye contact.

Color change probably has a thermoregulatory as well as a concealment function in *Cyclura*. The equation of Hutchison and Larimer (1960)

was used to estimate the mean heat gain of dorsal skin patches exposed to direct solar radiation:

$$\bar{H} = R(\frac{A}{100}) \qquad (6)$$

where $\bar{H}$ is the mean heat gain in langleys ($cal \cdot cm^{-2} \cdot min^{-1}$), R is the energy content of solar radiation between 400 and 1100 nm equal to 1.07 langleys for an air mass of one (high transmission), and A is the mean percent absorption of the skin patch over the same spectral range. The mean heat gains for dorsal abdominal skin patches from lizards in their light and dark phases were 0.763 and 0.919 langleys, respectively. The light phase value fell in the range found by Hutchison and Larimer for four desert lizard species ($\bar{X}$ = 0.747, range = 0.685-0.818). Two of these lizards were iguanines, *Dipsosaurus dorsalis* and *Sauromalus obesus*. The dark phase value fell in the range of their six forest species ($\bar{X}$ = 0.948, range = 0.898-0.990). The rates of heat gain were estimated to be 0.78 and 0.92 C/min for lizards in their light and dark phases, respectively, a difference of 15.3 percent. These data are for a 964 g animal in a walking posture (surface area = 1034 cm^2, assumed to be the same as a *Sauromalus obesus* of the same weight; T_b = 36 C) on a level, light sand substrate (T_s = 40 C) in still air (T_a = 30 C) on a clear day, calculated using Norris' technique (1967, pp. 209-210).

Melanin was deposited sparingly between some muscle blocks and more abundantly in the epidermis and the dermis just peripheral to the muscle layer. Peritoneal melanization increased as the thickness of the overlying musculature decreased: 1. the peritoneum was lightest dorsally, where the epaxial musculature was thickest, darker ventrally, and darkest in a clearly defined lateral band, 2. the peritoneum was lighter in the pleural than the abdominal cavity, 3. juveniles had

darker peritoneums than adults. Porter (1967) demonstrated that the black peritoneum helped absorb ultraviolet light (spectral range = 290-400 nm) before it could penetrate and possibly mutagenically damage the viscera.

The Integument: Sensory Spots

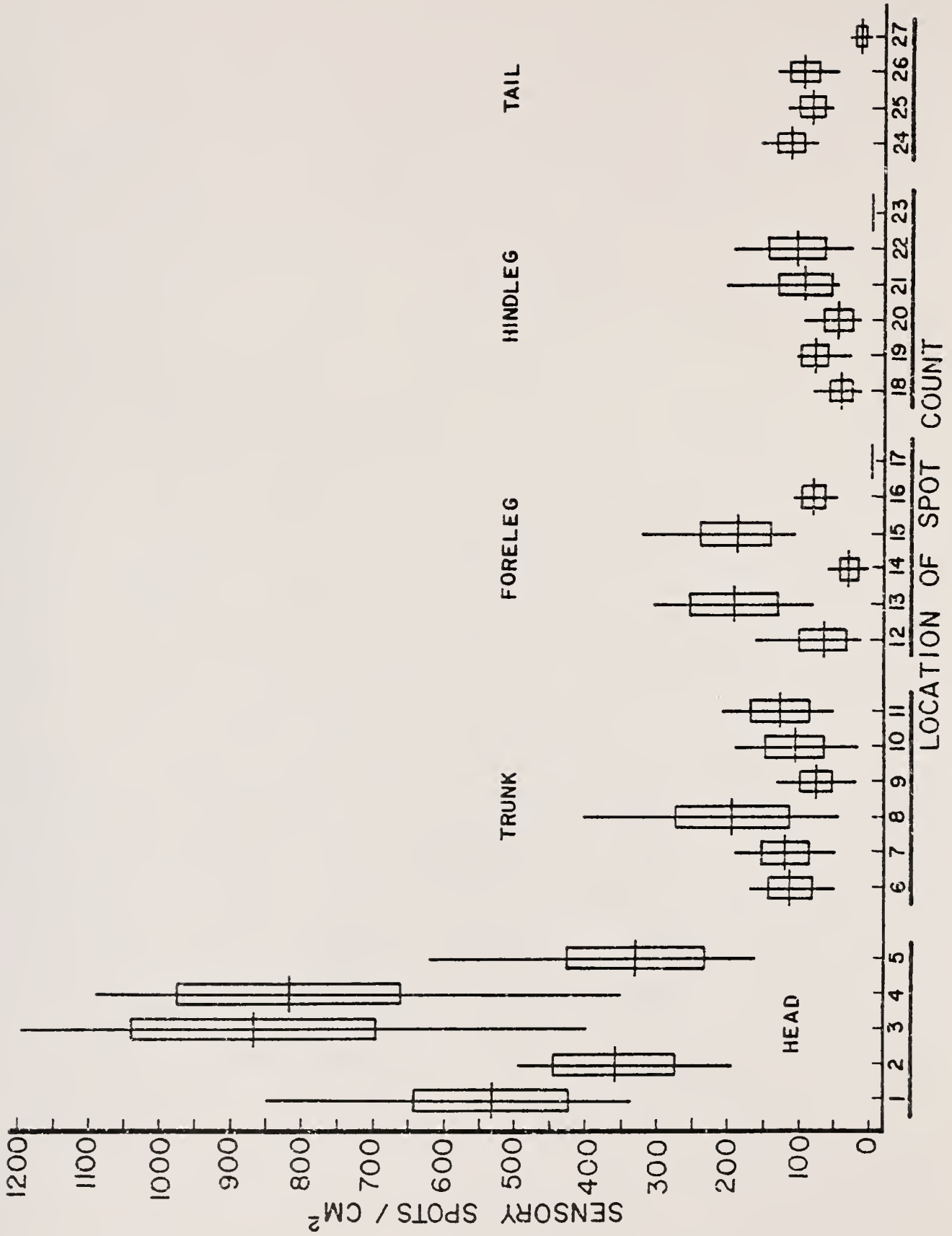
Specialized "tactile" or "sensory" spots have been described for the integument of a wide variety of reptiles (Mauer 1895, Jaburek 1926). In general, the epidermal cells are more columnar than in the surrounding unspecialized areas, and the overlying inner alpha- and outer beta-keratin layers are variously modified (Miller and Kasahara 1967). I found spots in all representatives of 21 iguanid genera examined, most numerously in the nine iguanine genera. Spots in *Cyclura carinata* numbered from zero to +500 per scale, located on different areas of scales from different parts of the body. They were circular, peglike, flat to slightly domed superficially, and 0.1 to 0.2 mm in diameter. Each spot consisted of a dermal papilla covered with a stratified columnar epithelium and extended above the living cells of the rest of the epithelial surface. The surface of the peg was covered with a thin layer of alpha-keratin, slightly thinner than over the rest of the epithelium. The outer beta-keratin layer only extended up to the side of each peg, not forming a "lens-like" cap on top as reported for *Varanus bengalensis* (Miller and Kasahara). The outer flat or slightly domed alpha-keratin-covered peg surface was practically continuous with the surface of the surrounding beta-keratin. In the living animal, the peg may be slightly elevated above the rest of the integumental surface. Faint traces of nerve fibers were detected in the

hematoxylin-eosin stained preparations, extending from the dermal papilla into the sensory epithelium.

As in other iguanids, spots were concentrated on the head. They were especially numerous on the rostral ($\bar{X}$ = 2100 spots/cm^2, N = 8, SD = 143, range = 1950-2400), mental, and labial scales (Figure 62). Spots were absent from the palmar and plantar surfaces of the feet, perhaps due to the likelihood of abrasive damage by hard substrates. Spot densities were generally higher on the ventral sides of the trunk and legs, the reverse on the tail.

Sensory spots most likely serve as touch or pressure receptors (mechano-receptors) in *Cyclura*, since they are concentrated at common contact points with external objects: the snout with objects during locomotion and rest, the lips with leaves, fruits, and other iguanas during male-male fighting, the ventral anterior trunk with objects during basking and with three trunks during climbing, and the ventral forelimbs with branches during climbing and with other iguanas during mating. It is also possible that sensory spots serve a thermal sensory function. They have been suggested to be radiant heat receptors in the Varanidae (Miller and Kasahara) and the Rhynchocephalian, *Sphenodon punctatus* (Maderson 1968). Berk and Heath (1975b) observed jaw rubbing in *Dipsosaurus dorsalis* similar to that seen in *Cyclura* in the same context; lizards were in the minimum T_b range of the regulating phase and just about to initiate a shuttling movement to the hot end of the thermal gradient. They suggested that jaw rubbing either served as a displacement activity or for substrate temperature sensing. The higher ventral trunk and leg concentration of sensory spots may be related to

Figure 62. Density of sensory spots on different parts of the lizard body surface. Spot densities were determined at the following locations: Head 1) dorsally on and around the parietal eye, 2) laterally just anterior to the tympanum, 3) upper lip, 4) lower lip, 5) ventrally between the mandibular rami; Trunk 6) anterior dorsal, 7) anterior lateral, 8) anterior ventral, 9) posterior dorsal, 10) posterior lateral, 11) posterior ventral; Forelegs 12) dorsal upper arm, 13) ventral upper arm, 14) dorsal forearm, 15) ventral forearm, 16) dorsal forefoot, 17) palm; Hindlegs 18) dorsal thigh, 19) ventral thigh, 20) dorsal calf, 21) ventral calf, 22) dorsal hindfoot, 23) plantar surface; Tail 24) dorsal proximal, 25) ventral proximal, 26) dorsal distal, 27) ventral distal. The sample consisted of eight adult lizards. Horizontal lines are means, vertical lines are ranges, and rectangles are plus and minus two standard errors of the mean.


SENSORY SPOTS / CM²
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
HEAD
TRUNK
FORELEG
HINDLEG
TAIL
1 2 3 4 5
6 7 8 9 10 11
12 13 14 15 16 17
18 19 20 21 22 23
24 25 26 27
LOCATION OF SPOT COUNT

two other possible thermal sensory behaviors, sand swimming and hard substrate rubbing with the ventral body surface.

PHYSIOLOGICAL ASPECTS OF THE THERMAL BIOLOGY OF *CYCLURA CARINATA*

Heating and Cooling Rates

With constant air temperature and wind speed, low relative humidity, and substrate and wall temperatures equaling air temperature, Newton's law of cooling adequately describes lizard body temperature change:

$$\frac{dT_b}{dt} = -A(T_b - T_a) \tag{6}$$

Integration and rearrangement yields:

$$\ln(T_b - T_a) = -at + k \tag{7}$$

where t is time in minutes, a is a cooling constant in min^{-1}, and k is an integration constant. Plotting $\ln(T_b - T_a)$ vs. t yields a straight line with the cooling constant as the slope. The apparent thermal conductance ($cm^3O_2 \cdot g^{-1} hr^{-1} \cdot °C^{-1}$) is then estimated from the equation:

$$C' = \frac{a \cdot H_s \cdot 60}{E} \tag{8}$$

where H_s is the approximate specific heat of lizard tissue (0.82 $cal \cdot g^{-1} \cdot C^{-1}$) and E is the caloric equivalent of a cubic centimeter of oxygen (4.8 $cal \cdot cm^{-3}O_2$) assuming a respiratory quotient of 0.85. C' is an apparent conductance since the effect of metabolic heat production is not accounted for. A corrected C can be calculated by using the following equation (Bartholomew and Tucker 1963):

$$C = C' \pm \frac{M}{T_b - T_a} \tag{9}$$

where M is the metabolic rate ($cm^3O_2 \cdot g^{-1} \cdot hr^{-1}$) during a cooling ($+M/(T_b - T_a)$) or heating ($-M/(T_b - T_a)$) run. There is some question whether this later technique is correct (Strunk 1971).

Iguanas heated faster than they cooled both in the cage and on the jig (Figure 63 and Table 20). The low slope of the line during the initial twenty minutes of heating on the jig may have been caused by a fear-induced bradycardia. This has been reported in *Alligator mississippiensis* (Smith 1976). Lizards almost always heated and cooled more slowly in the cage, undoubtedly due in part to the greater leg and ventral trunk contact with the substrate than when resting on the narrow wooden strip of the jig. However, the rates were not significantly lower in the cage ($p > 0.05$, student t-test). The mean cooling/heating conductance ratio was less in the cage than on the jig, but again the difference was not significant. Apparently, some lizards thermoregulated behaviorally in the cages, increasing their heating rates by minimizing substrate contact and decreasing their cooling rates by maximizing contact. The mean C/H ratio might have been significantly less in the cages had the lizards been habituated to their surroundings for a longer time.

The uncorrected C/H ratio at 30 C for a single *Amblyrhynchus cristatus* (0.52, wind speed = 113 cm/sec, Bartholomew and Lasiewski 1965) is the only lizard value reported in the literature that is less than the lowest jig value for *Cyclura carinata*, 0.62. The ratios for two *Amphibolurus barbatus* in still air, 0.64 and 0.71 (Bartholomew and Tucker 1963) are similar to *Cyclura* cage and jig means, 0.66 and 0.72, respectively. *Dipsosaurus dorsalis* in still air ($\bar{X} = 0.88$, Weathers 1970), four varanid species at wind speeds of 230-300 cm/sec ($\bar{X} = 0.88$, Bartholomew and Tucker 1964), and *Tiliqua scincoides* at 136-156 cm/sec

Figure 63. Heating and cooling rates of a 1435 g male *Cyclura carinata* in a constant temperature chamber. The lizard (Number 4 in Table 20) was heated (solid circles) and cooled (open circles) on a jig and heated (solid triangles) and cooled (open triangles) in a cage located in a constant temperature chamber set at 40 and 20 C, respectively. Regression lines were fitted to the points by the method of least squares. The low slope of the initial jig heating line may be due to a fear-induced bradycardia (B).

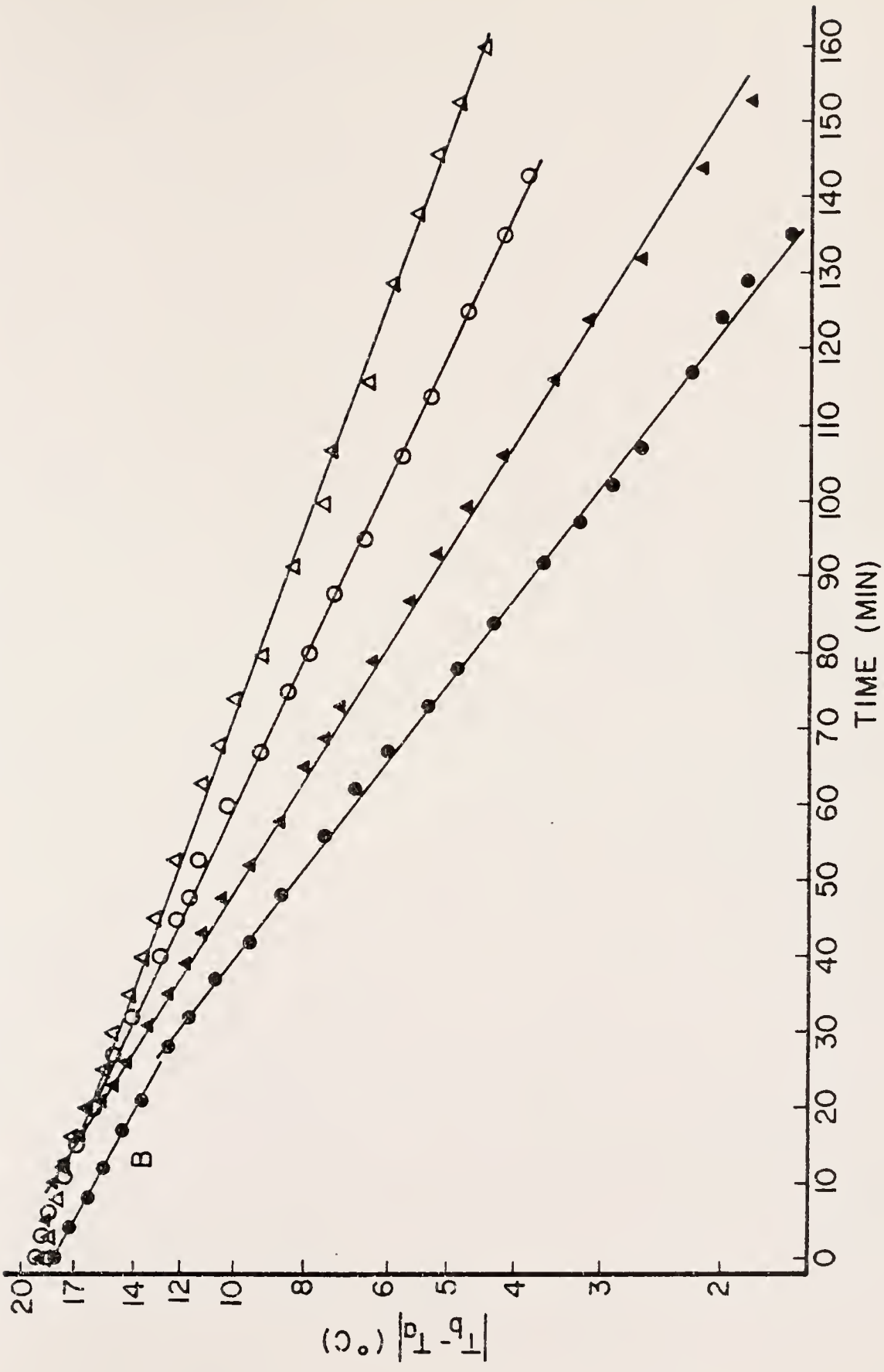

20
17
14
12
10
8
6
5
4
3
2
B
$|T_b - T_a|$ (°C)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
TIME (MIN)

Table 20. Estimated thermal conductance ($cm^3O_2 \cdot g^{-1} \cdot hr^{-1} \cdot °C^{-1}$) during heating and cooling of lizards in still air.

A. UNCORRECTED FOR METABOLISM

		ON JIG			IN CAGE		
Lizard	Weight (g)	Heating	Cooling	C/H	Heating	Cooling	C/H
1	810	0.229	0.176	0.768	0.236	0.159	0.674
2	812	0.221	0.164	0.742	0.208	0.136	0.654
3	895	0.215	0.140	0.651	0.183	0.112	0.612
4	1435	0.195	0.121	0.621	0.164	0.095	0.579
5	1472	0.191	0.132	0.691	0.135	0.098	0.726
6	1510	0.154	0.131	0.851	0.144	0.101	0.701
$\bar{X}$	1156	0.201	0.144	0.721	0.178	0.117	0.658
SD	349	0.027	0.021	0.084	0.039	0.025	0.055

Table 20. Continued.

B. CORRECTED FOR METABOLISM

Metabolic Rate Correction	Body Temperature 25 C	30 C	35 C
I. RESTING METABOLIC RATE[1]			
		C/H ($\bar{X}$ and Range)	
Jig:	0.827(0.719-0.981)	0.812(0.699-0.963)	0.900(0.767-1.078)
Cage:	0.779(0.698-0.872)	0.759(0.671-0.848)	0.857(0.751-0.919)
II. CONDUCTANCE DURING HEATING = CONDUCTANCE DURING COOLING			
		Required M/Resting M and Required M/Maximum M ($\bar{X}$ and Range)	
Jig:	2.54(1.13-3.58) & 0.61(0.24-0.80)	2.84(1.34-4.16) & 0.62(0.25-0.82)	1.46(0.68-2.14) & 0.38(0.15-0.49)
Cage:	2.73(1.81-3.17) & 0.66(0.39-0.82)	3.04(2.10-3.88) & 0.67(0.41-0.84)	1.56(1.09-1.74) & 0.41(0.24-0.51)
III. MAXIMUM METABOLIC RATE[2]			
		C/H ($\bar{X}$ and Range)	
Jig:	1.219(1.094-1.534)	1.250(1.100-1.639)	2.318(1.762-4.225)
Cage:	1.240(1.075-1.500)	1.278(1.079-1.618)	3.235(1.615-6.476)

[1]The equations relating resting metabolism ($cm^3O_2 \cdot g^{-1} \cdot hr^{-1}$) to body weight (N = 5 lizards, mean weight = 1252 g, range = 834-1722 g) were $M_{25C} = -0.0000217\ W + 0.109$ ($r = -0.450$, not significant at $p \leq 0.05$), $M_{30C} = -0.0000395\ W + 0.146$ ($r = -0.926$, significant at $p \leq 0.025$), and $M_{35C} = -0.0000574\ W + 0.212$ ($r = -0.821$, significant at $p \leq 0.05$).

[2]No correlation was found between maximum oxygen consumption and body weight in the five lizards above (Footnote 1). Therefore, only one maximal metabolic rate corrected was used at each body temperature, calculated from the equation, Log M_{max} = 1.425 Log T_b - 2.446 (N = 5 lizards, T_b = 13-43 C).

(0.85 and 0.90, Bartholomew *et al.* 1964) all have *C/H* ratios closer to unity than *Cyclura*. Weathers (1970) demonstrated that the ratio was independent of body weight in *Dipsosaurus*, partially justifying the above comparisons. However, he also found that the ratio increased slightly as wind speed increased.

Weathers (1972) found that increasing water vapor pressure in the controlled temperature room had no effect on the cooling rate of *Dipsosaurus* but markedly increased its heating rate. He hypothesized that water condensed on the lizard's skin at body temperatures below the dew point, adding the latent heat of fusion to the conductive and convective heating of the air. Water evaporating from the skin surface above the dew point would reduce the heating rate. This change in heat input was evident in the nonlinear heating rate of these small lizards. Water condensed on the skin when relative humidity was above 31.8 percent, a value undoubtedly exceeded in my experiments. Unfortunately, no attempt was made to control nor even measure relative humidity during heating and cooling of *Cyclura*. Neither were any lizards killed for use as heating and cooling controls. However, jig heating curves were all practically linear. Also, any water vapor effect should be less in *Cyclura* than the smaller *Dipsosaurus*.

No investigator has concurrently measured oxygen consumption and heating vs. cooling rates in lizards. Bartholomew and Tucker (1963, 1964) and Bartholomew *et al.* (1965) measured heart rates during heating and cooling and during oxygen consumption at several body temperatures, then assumed the metabolic rate from the appropriate heart rate. Since neither heart rate nor oxygen consumption was measured during heating and cooling in the present study, three metabolic corrections have been

calculated: I. resting metabolic rate, II. the fraction of resting and maximum rates which equalized heating and cooling rates, and III. maximum metabolic rate (Table 19). In no case did the resting metabolic rate correction totally account for the low *C/H* ratios. However, lizards were completely quiet during only 33 percent of the runs. Struggling on the jig and climbing the walls of the cage occurred during ten and three of twelve runs, respectively. Lizards were also disturbed during chamber switching. Thus, it is unlikely that any lizard metabolized at its resting rate during heating or cooling. The maximum metabolic rate correction more than corrected for the faster heating rates. However, lizards could not have sustained a near maximum rate for the duration of the run, an average of 148 minutes during heating and 156 minutes during cooling. The question is, at a T_b of 30 C, for example, whether lizards averaged more or less than approximately three times resting or two-thirds maximum oxygen consumption. An unrealistically high metabolic correction, 82 percent of maximum on the jig and 84 percent of maximum in the cage, would be required to equalize the rates for lizards with the smallest *C/H* ratios. Thus, *Cyclura* probably has some physiological control of its heating and cooling rates.

In the jig, the *C/H* ratio (Y) was directly related to the ratio of struggling bouts during cooling vs. heating (X), with the equation: $Y = 0.04809\ X + 0.6671$ ($r = 0.800$, $p \leq 0.025$, $N = 7$). This was expected, since the more struggling that occurred during cooling relative to heating, the greater the relative difference in metabolic heat production at any one T_b. The *C/H* ratio was not correlated with the ratio of escape attempts or escape attempts plus walking during cooling vs. heating in the cage. Perhaps, behavioral thermoregulation overrode brief

behaviors which increased the cooling rate. However, in one small iguana, data not included in Table 20, the *C/H* ratio was 1.496 in the cage, clearly due to escape attempts during cooling.

Climbing and walking in the cage and struggling on the jig occurred at significantly higher temperatures during heating than during cooling (Table 21). This was partly due to the greater amount of time the lizards were at high T_b's during heating than during cooling. Also, lizards were actively trying to avoid different unfavorable thermal conditions during heating and cooling, near the maximum and minimum voluntary tolerances, respectively. The first defecation during heating occurred at 5.0 C above the last defecation during cooling, following the pattern for climbing (11.6 C), walking (1.7 C), and struggling (5.6). Lizards relaxed on the substrate to the level of the pectoral girdle at a higher T_b during cooling than during heating, although the difference was not significant. Head contact with the substrate occurred for brief periods only during cooling. This increased substrate contact undoubtedly decreased the cooling rate. Gular flutter ceased an average of 9.7 C lower during cooling on the jig than in the cage. Participation of the intercostal muscles in inhalation was probably reduced by the jig restraining strap, located immediately posterior to the forelegs, to the point that supplementary gular flutter was necessary for adequate respiration at low T_b's.

Only two of seven restrained lizards and none of the caged lizards panted during heating. One animal panted at the end of the run at a T_b of 39.0 C. The other, Number 3 in Table 20, started at 32.8 C and continued intermittently during 30.9 percent of the remainder of the run. The lizard also struggled six times.

Table 21. Correlations of lizard behaviors with body temperature during heating and cooling in the cage and on the jig.

BEHAVIOR	HEATING OR COOLING	CAGE OR JIG	$\bar{X}$ T_B	RANGE	SD	SD_{COOL}/SD_{HEAT}	N/7 LIZARDS	SIGNIFICANCE LEVEL[1]
Climbing	Heating	Cage	37.0	34.5-38.3	1.524	2.49	8	0.005
Climbing	Cooling	Cage	31.6	22.9-37.5	3.800		19	
Walking	Heating	Cage	36.4	24.6-38.3	2.952	1.45	25	0.005
Walking	Cooling	Cage	31.2	22.9-38.2	4.276		45	
Defecation	Heating	Cage	37.2	34.1-38.7	1.763	2.09	5	NS
Defecation	Cooling	Cage	33.8	29.1-37.6	3.682		6	
Struggling	Heating	Jig	35.4	29.3-38.3	2.625	1.74	22	0.005
Struggling	Cooling	Jig	31.4	23.6-38.6	4.564		24	
Pectoral Girdle Contacts Substrate	Heating	Cage	33.9	28.8-37.2			7	NS
	Cooling	Cage	36.3	31.9-38.5			7	
Head Contacts Substrate	Cooling	Cage	31.7	27.0-36.8			4	
Starts Gular Flutter	Heating	Cage	35.0	32.1-37.6			7	NS
	Heating	Jig	32.4	24.6-37.9			7	
Stops Gular Flutter	Cooling	Cage	33.4	32.1-34.6			7	0.005
	Cooling	Jig	23.7	23.0-25.7			7	

[1] Student t-test for difference in $\bar{X}$ T_b's.

Breathing rates were significantly higher during heating than during cooling in both the cage and on the jig (Figure 64). Only one caged lizard had about equal breathing rates. The difference may be due to thermal hysteresis. Head temperature probably increased faster than intestinal temperature during heating and decreased faster than intestinal temperature during cooling. Thus, for any one intestinal temperature, brain temperature may be considerably higher during heating. Since the respiratory center is located in the hypothalamus and direct heating of the area, at least in cats (Nakayama *et al.* 1963) leads to an increased respiratory rate, thermal hysteresis may account for the breathing rate difference. A direct temperature effect on the firing rate of lung stretch receptors may also be involved. Reduced tidal volume due to restraint may have caused the higher mean breathing rate during cooling in the jig than in the cage. Mean breathing rate ratios of individual lizards during heating and cooling were uncorrelated with their respective conductance ratios. Thus, unless the convective heat gain through the lungs during heating and the lower convective heat loss during cooling were offset by higher and lower evaporative cooling, respectively, the difference in respiratory rates did not contribute significantly to the higher lizard heating rates.

The breathing rate during heating in the cage was highly temperature dependent between 22 and 30 C (Q_{10} = 4.32) and became nearly temperature dependent between 30 and 38 C (Q_{10} = 1.18), almost encompassing the preferred T_b range. The rate was moderately temperature dependent over the full cooling range in the cage (Q_{10} = 2.57 from 38 to 30 C, 2.12 from 30 to 22 C). Lizards were occasionally apneustic (6 of 14 runs) when

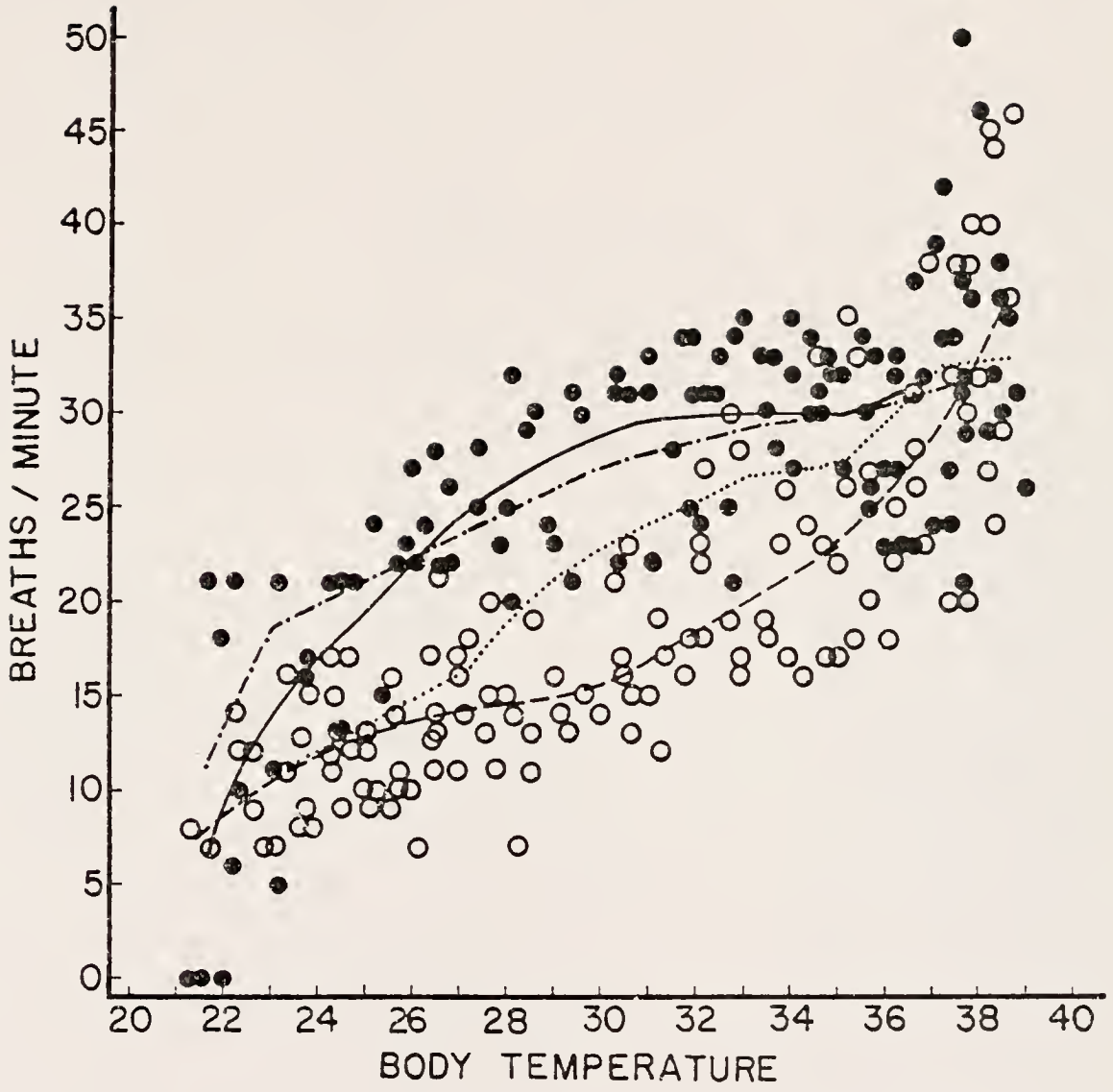


Figure 64. Breathing rates of lizards during heating and cooling in a constant temperature chamber. The solid circles and solid line refer to the rate during heating, open circles and dashed line to the rate during cooling in the cage. The dot and dash and dotted lines refer, respectively, to heating and cooling respiratory rates on the jig. Lines are running means for six animals.

first placed in the 40 C chamber but rarely so at any other time (1 of 28 runs).

Aerobic Metabolism

A semilog plot of resting metabolism ($cm^3O_2/g \cdot hr$) vs. T_b was fitted to a straight line (Figure 65):

$$\text{Log } M_r = 0.0322\ T_b - 2.003$$
$$(N = 30,\ 13.4 \leq T_b \leq 43.0\ C,\ r = 0.954) \qquad (10)$$

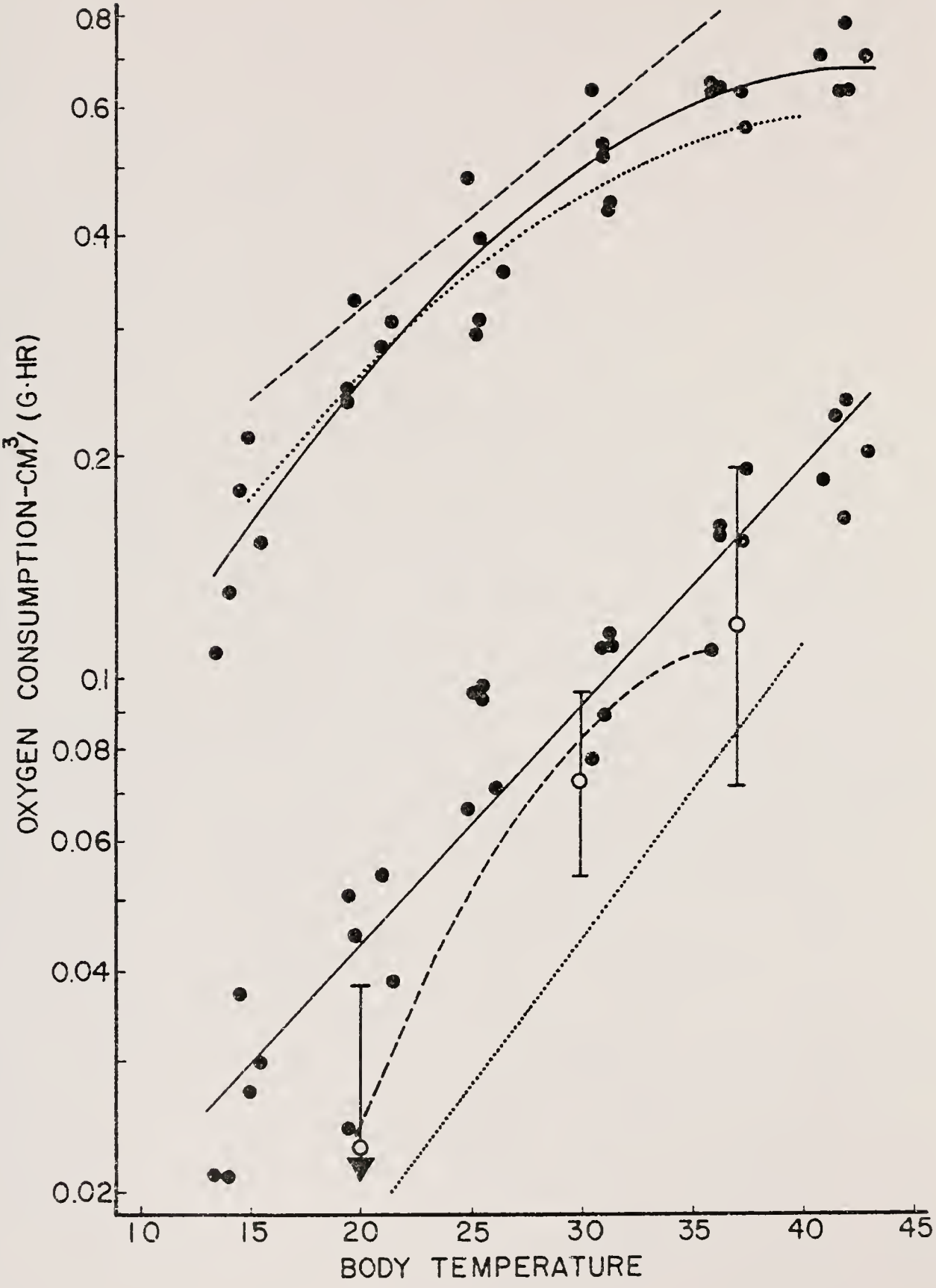
Resting oxygen consumption in *Cyclura* was slightly greater than in *Sauromalus hispidus* and *Varanus gouldii* weighing about half as much, on the average (Bennett 1972). The *Cyclura* line was also above points plotted for a 1252 g lizard using equations for body weight vs. resting metabolism calculated for many lizard species (Bennett and Dawson 1976). However, the positive 95 percent confidence limits for their 30 and 37 C equations do exceed the *Cyclura* line. The iguanas may not have fully recovered from exercise before resting rates were taken, may have been acclimatized to lower environmental temperatures (late autumn in Gainesville), or been stressed by the face mask. Hutchison *et al.* (1977) reported lower resting oxygen consumption in *Ambystoma trigrinum* when tested in an all body chamber rather than with a face mask.

The log of a maximum oxygen consumption vs. T_b was best fitted to a second degree polynominal, using the statistical technique of Mills (1955):

$$\text{Log } M_a = -0.00076\ T_b^2 + 0.0662\ T_b - 1.6128$$
$$(N = 30,\ 13.4 \leq T_b \leq 43.0\ C,\ r = 0.965) \qquad (11)$$

Maximum oxygen consumption occurred at 43-44 C, a 1 C extrapolation above the data. *Sauromalus* and *Cyclura*, relatively sluggish herbivores, had similar curves lying below the linear plot of *Varanus*, an active carnivore.

Figure 65. Correlation of resting and maximum oxygen consumption with body temperature. Solid lines and circles refer to *Cyclura carinata* ($\bar{X}$ weight = 1252 g, N = 5, each animal run at six T_b's). Regression lines were constructed using equations (10) and (11). Values for *Sauromalus hispidus* (dotted lines, $\bar{X}$ weight = 574 g) and *Varanus gouldii* (dashed line, $\bar{X}$ weight = 674 g) were included for comparison (Bennett 1972). The resting metabolic rates (open circles) and plus and minus the 95 percent confidence limit (vertical lines) were calculated for a 1252 g lizard from equations based on many lizard species (Bennett and Dawson 1976).


0.8
0.6
0.4
0.2
0.1
0.08
0.06
0.04
0.02
OXYGEN CONSUMPTION-CM3/(G·HR)
10
15
20
25
30
35
40
45
BODY TEMPERATURE

Due to metabolic heat production, *Cyclura* T_b's measured immediately after seven minutes of activity were nearly always above the air temperature of the chamber (mean $T_b - T_a$ difference = 0.8 C, range = -0.6 to 1.9 C, $T_a = 0.987\ T_b - 0.398$).

The Q_{10} for resting metabolism was constant at 2.10, lacking an adjustment toward temperature independence at the preferred T_b range (Figure 66). This is a fairly common characteristic of lizards (Bennett and Dawson 1976). Unfortunately, M_r was not measured at 5 and 10 C. A significant increase in Q_{10} would be expected in this T_b range in a heat tolerant species (Dawson 1967). The Q_{10} for maximum metabolism declined from 2.49 between 15 and 20 C to 1.07 between 40 and 43 C. This shift from temperature dependence below the preferred range to temperature independence at and above the preferred range is characteristic of all lizards studied thus far, except for several varanids (Bennett and Dawson 1976). Over most of the T_b range, the thermal sensitivity of the maximum metabolic rate was less than that of the resting metabolic rate.

The M_m/M_r ratio or factorial scope nearly reached six between T_b's of 20 and 25 C, then declined steadily above 25 C (Figure 66). The maximum ratio occurred slightly below body temperature of morning emergence. Increments of five to six-fold at 30 C and three to six-fold at preferred body temperature were typical for lizards (Bennett and Dawson 1976).

The aerobic scope for activity, determined by subtracting the resting from the maximal metabolic rate at a particular T_b, is a useful index of the capacity of a species to support a bout of activity with energy derived from oxygen-dependent pathways. *Cyclura*'s maximum

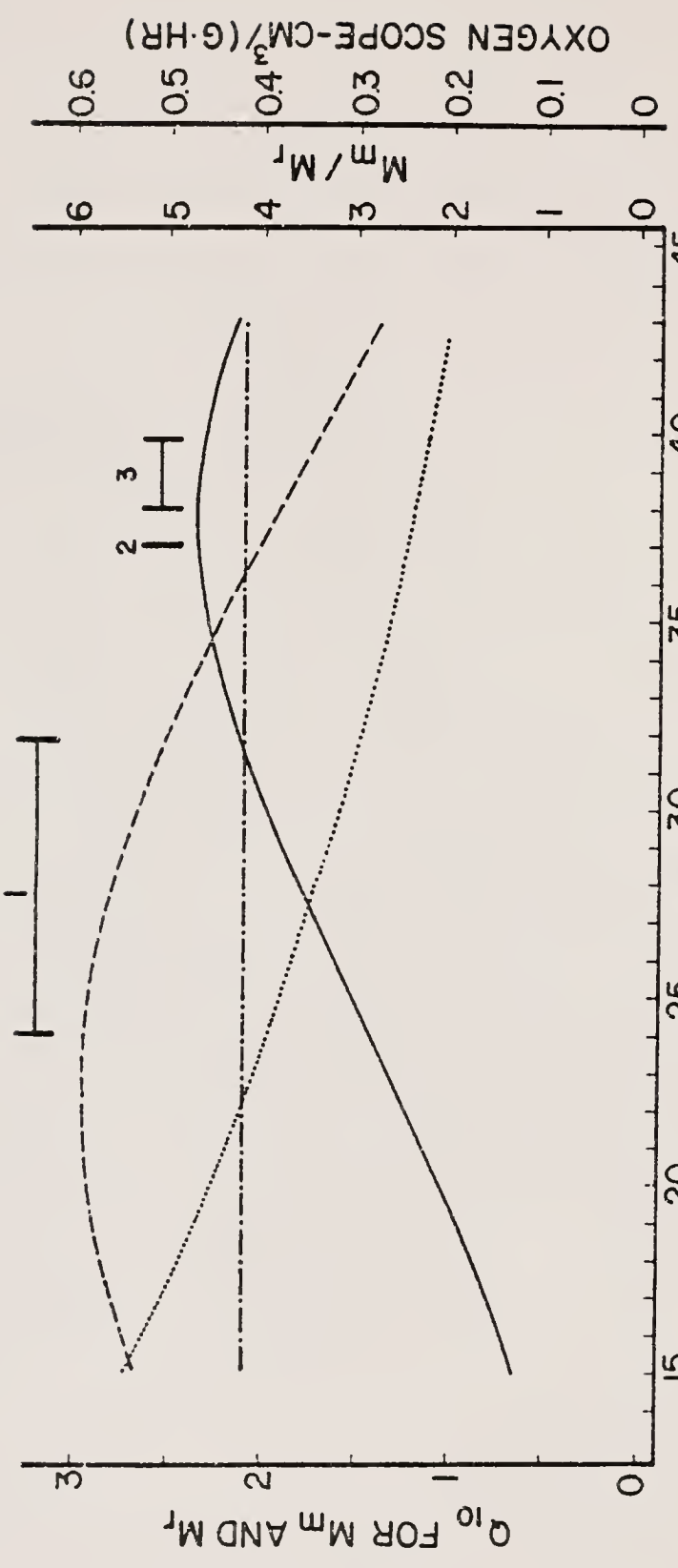


Figure 66. Analysis of aerobic metabolism. Oxygen consumption Q_{10}'s for resting (dot and dash line) and maximally active lizards (dotted line), the ratio of maximum to resting metabolism (dashed line), and aerobic scope (solid line) are displayed. Horizontal lines and numbers refer to the ranges of: 1) emergence T_b's, 2) mean preferred T_b, and mean regulating phase T_b's in the field.

aerobic scope occurred between 37 and 39 C [maximum at a T_b of 38.1 C; 0.47 $cm^2/(g \cdot hr)$], corresponding well to its preferred T_b of 37 C (Figure 66). This correspondence has been demonstrated for several other lizards (Wilson 1974, Bennett and Dawson 1976), but not for varanids (Bennett 1972) nor two turtles (Gatten 1974a). Aerobic scope declined to 28 percent of maximum at 15 C, 2.3 C above the critical thermal minimum, and extrapolated to 22 percent of maximum at the CTMin. At T_b's of 40 C, scopes for *Sauromalus hispidus* and *Cyclura carinata* were about half that of the more active *Varanus gouldii* [0.47, 0.47, and 0.89 $cm^3/(g \cdot hr)$, respecively; Bennett 1972]. Nonetheless, the predicted scope for reptiles at a T_b of 30 C and at preferred T_b (Gatten 1978, based on 20 species) were only 86 and 69 percent of the actual values for *Cyclura* [predicted scopes of 0.340 and 0.324 $cm^3 O_2/(g \cdot hr)$ at 30 C and 37 C, respectively; actual values were 0.397 and 0.471; mean body weight was 1252 g]. Thus, the rock iguana can hardly be called a sluggish reptile, even though it is a herbivore.

Heart Rate

The points relating the log of resting heart rate to body temperature were best fitted to two straight lines meeting at a body temperature of 25.0 C (Figure 67):

$$\text{Log } HR_r = 0.0562\ T_b - 0.0122 \quad (N = 15,\ 13.4 \leq T_b \leq 26.2\ C,\ r = 0.903) \qquad (12)$$

$$\text{Log } HR_r = 0.0370\ T_b + 0.4461 \quad (N = 20,\ 24.9 \leq T_b \leq 43.0\ C,\ r = 0.955) \qquad (13)$$

Body temperature vs. maximum heart rate was fitted best by a second degree polynomial:

$$\text{Log } HR_m = -0.00069\ T_b^2 + 0.0782\ T_b + 0.0440 \quad (N = 30,\ 13.4 \leq T_b \leq 43.0\ C,\ r = 0.987) \qquad (14)$$

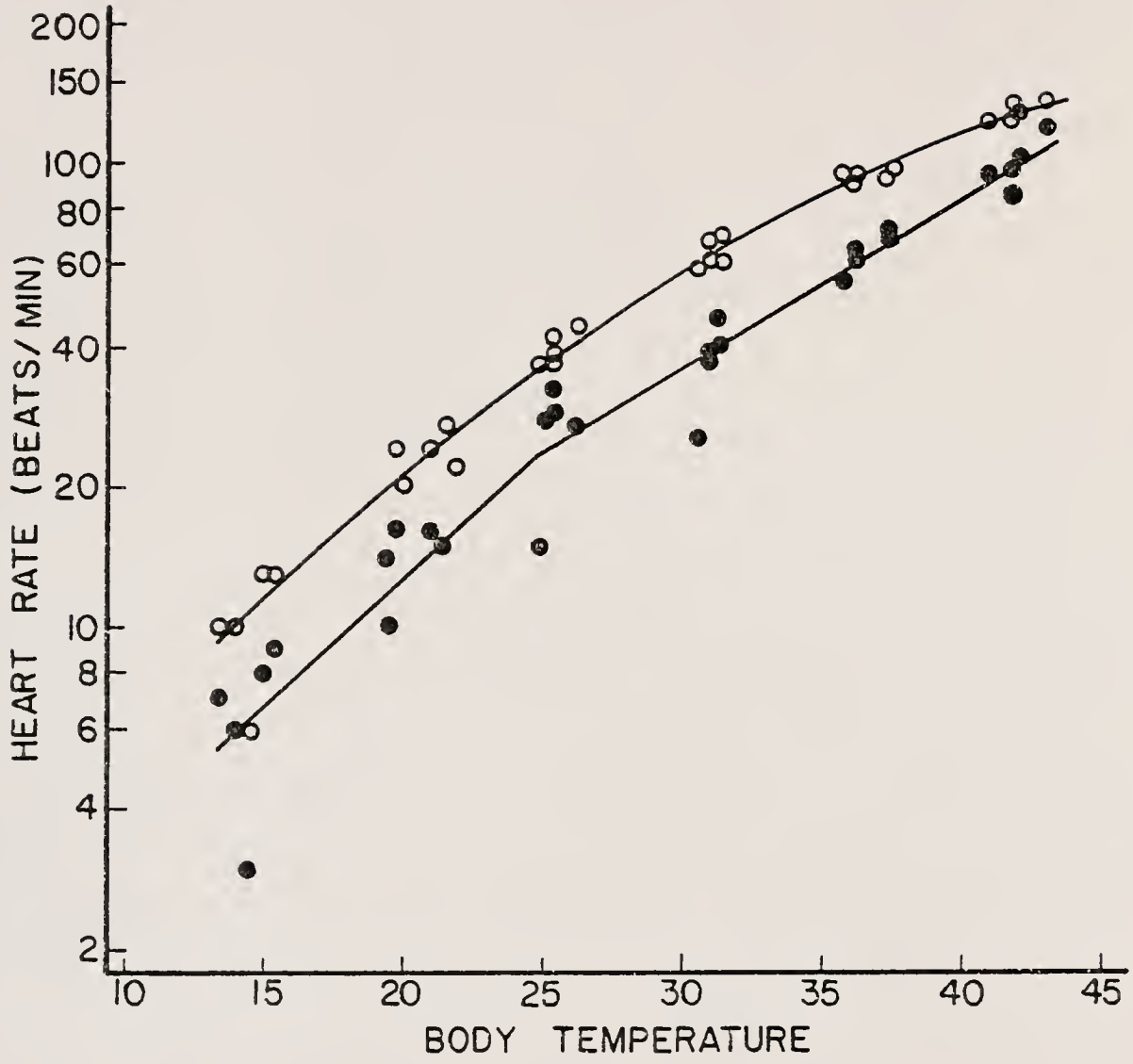


Figure 67. Heart rate as a function of body temperature. Maximum (open circles) and resting (solid circles) heart rates are plotted. Regression lines were constructed using equations (12)-(14).

The greatest resting and maximum heart rates were recorded at the highest body temperatures tested.

Resting heart rate Q_{10} was 3.63 between 15 and 25 C and 2.35 between 25 and 40 C (Figure 68). The Q_{10} change at 25 C fell in the range for emergence body temperatures and at an expectedly high T_b relative to more cold resistant lizards (Templeton 1970). The 3.63 value was slightly higher than in other lizard species monitored between body temperatures of 20 and 25 C (Q_{10} = 2.0-2.9: Templeton 1970, Wilson and Lee 1970, Burns 1971, Bennett 1972). The 2.35 value fell in the range found for other lizards between 25 and 40 C (Q_{10} = 1.8-2.5). Maximum heart rate increase declined steadily between 25 and 40 C but never reached the high level of body temperature independence achieved for oxygen consumption. The ratio of active to resting heart rate remained fairly constant at 1.56-1.69 between 13.4 and 35.0 C, then dropped to 1.24 at 43.0 C. The heart rate increment ($HR_m - HR_r$) was greatest at a T_b of 38.5 C, slightly above the mean preferred body temperature and within the range of mean field body temperatures. Licht (1965a) found a similar pattern in four lizard species.

According to the Fick equation, oxygen consumption under steady state conditions is equal to the product of heart rate, stroke volume, and the amount of oxygen extracted by the tissues (A-V difference). Oxygen pulse, defined as oxygen consumption divided by heart rate, is equal to the product of the stroke volume and the A-V difference. Resting oxygen pulse in *Cyclura* declined from 8.3×10^{-5} to 3.7×10^{-5} $cm^3 O_2/(g \cdot beat)$ between 13 and 43 C (Figure 69). The oxygen pulse during maximum activity declined rather precipitously from 24.9×10^{-5} to 8.3×10^{-5} between 13 and 43 C. Thus, *Cyclura* must be quite dependent on

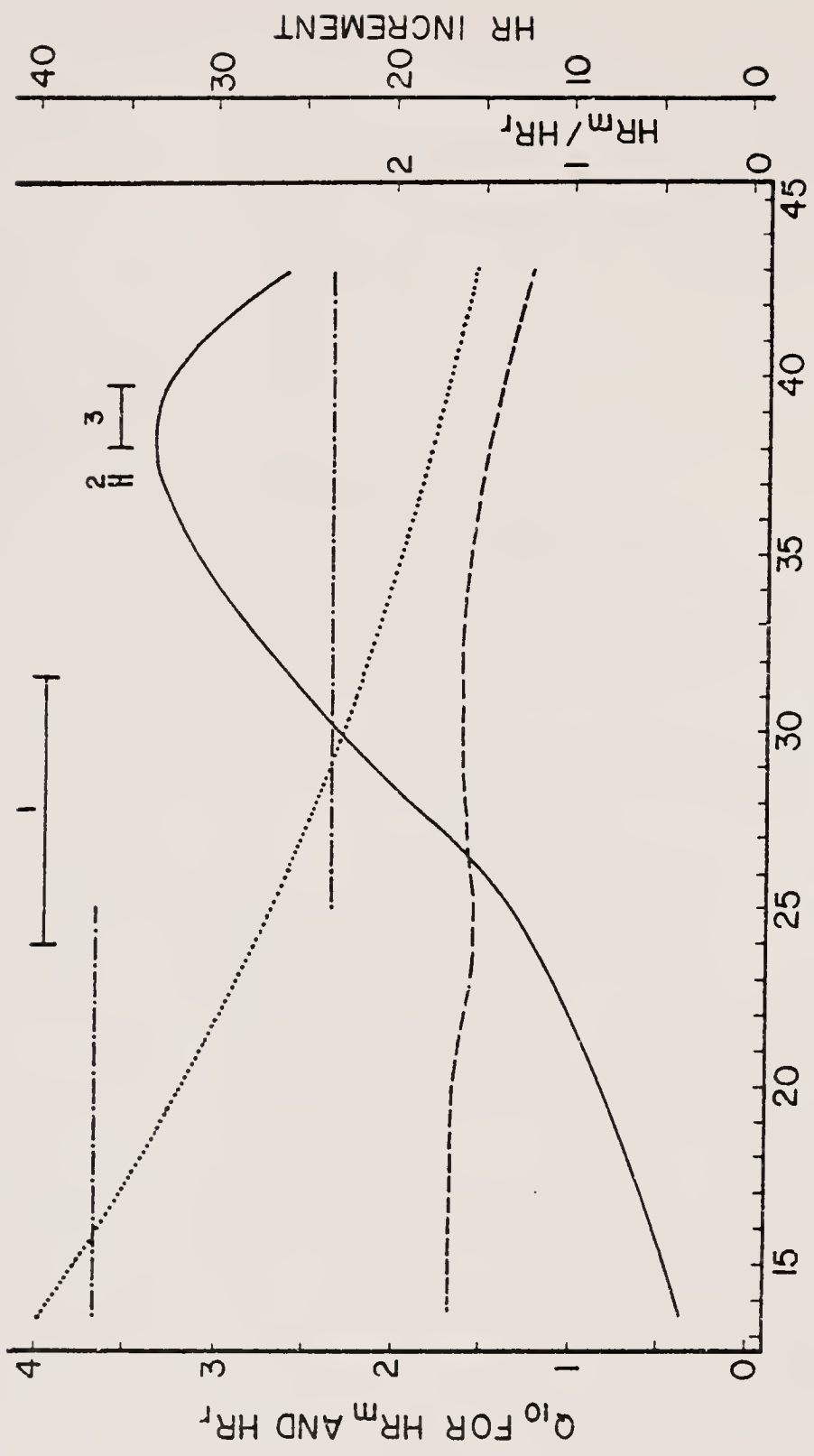


Figure 68. Heart rate analyses. Heart rate Q_{10}'s for resting (dot and dash line) and maximally active lizards (dotted line), the ratio of maximum to resting heart rate (dashed line), and the heart rate increment (solid line) are displayed. Horizontal solid lines refer to the ranges of: 1) emergence T_b, 2) mean preferred T_b, and 3) mean regulating phase T_b's in the field.

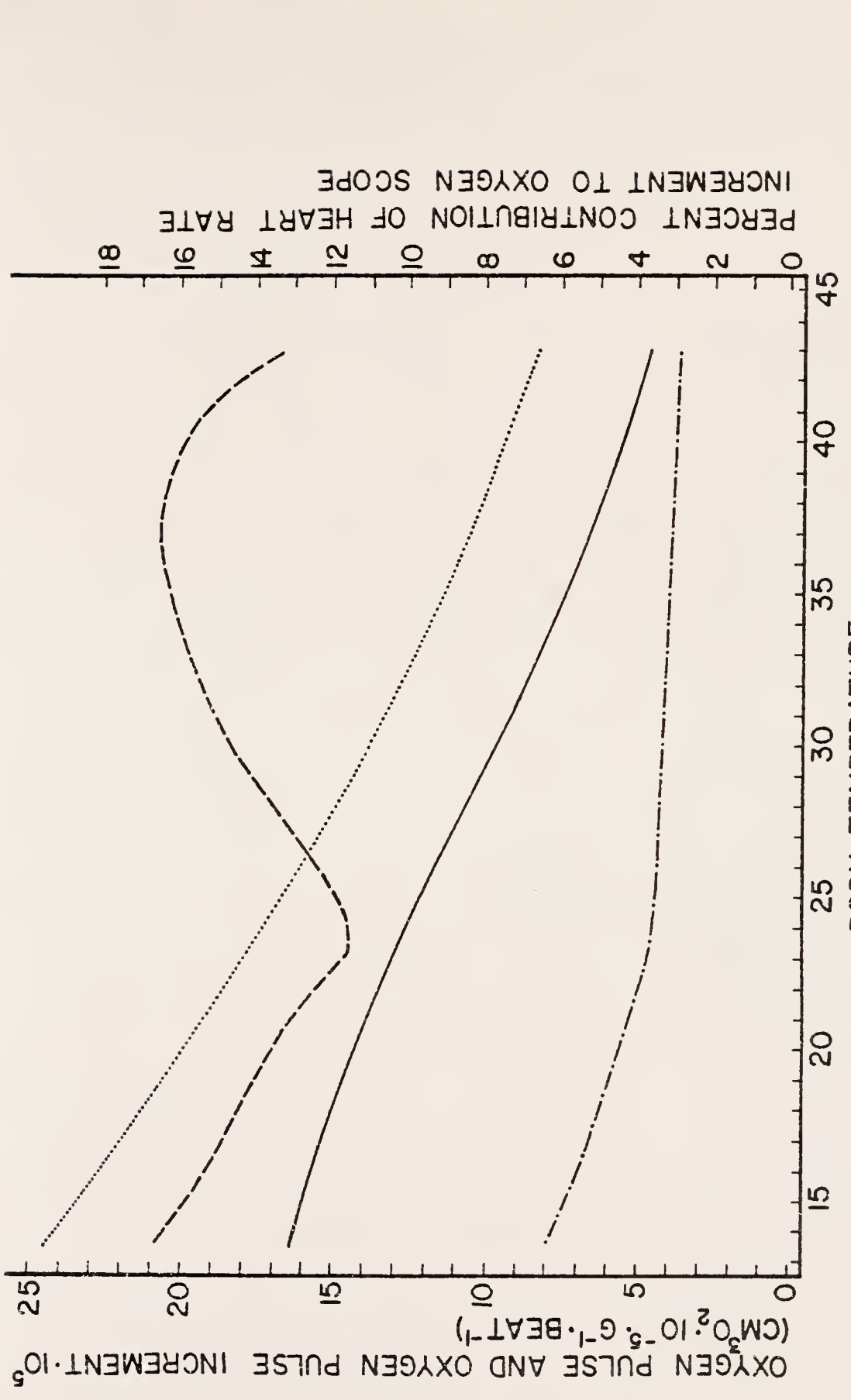


Figure 69. Relationship of oxygen consumption to heart rate at different body temperatures. Resting (dot and dash line) and maximally active (dotted line) lizard oxygen pulse, oxygen pulse increment (solid line), and the percent contribution of increased heart rate to increased oxygen transport during activity (dashed line) are plotted. Curves are constructed using equations (10)-(15).

increased heart rate to provide the increased oxygen demand of the tissues at higher T_b's, especially during activity. Since active oxygen pulse declined more rapidly than resting pulse as T_b increased, the oxygen pulse increment (active pulse - resting pulse) also declined. At 40 C, active pulse was only 2.5 times greater than resting pulse.

Gatten (1974b) proposed a correction to Bartholomew and Tucker's (1963) equation for the percent contribution of increased heart rate to increased oxygen transport during activity:

$$\text{Percent Contribution} = \left[\frac{(HR_a - HR_r)}{HR_r} \div \frac{(M_a - M_r)}{M_r} \right] \times 100 \qquad (15)$$

where HR_a, HR_r, M_a, and M_r are active and resting heart rates and active and resting metabolic rates, respectively. The curve calculated for *Cyclura* is plotted in Figure 69. Increased heart rate contributed the greater share vs. oxygen pulse for meeting increased oxygen demand during activity at T_b's of 13 and 37 and the smaller share at 24 C. The significance of the bimodal character of the curve, if any, is not known. The contribution of increased heart rate to satisfy the increased oxygen demand during activity is rather small in comparison to the contributions of stroke volume and A-V difference at any one T_b. This is in contrast to the importance of heart rate increase in satisfying increased oxygen demand as T_b increased oxygen transport during activity (15-40 at 5 C intervals, N = 6) using the Bartholomew and Tucker equation were 54.5 (49-65), 21.4 (17.2-24.4), and 14.8 (10-20) for *Sauromalus hispidus*, *Cyclura carinata*, and *Varanus gouldii* (Bennett 1972). Thus, the *Cyclura* values are considerably closer to *Varanus* than to *Sauromalus*. The two main reasons for this are the higher resting heart rate and higher maximum oxygen pulse of *Cyclura* than *Sauromalus*.

Recovery from Maximum Exercise

Struggling to escape was spontaneous during the first 1.5-2.0 minutes in the environmental chamber, maintained simply by holding the animal off the ground. The most numerous and powerful escape attempts, consisting of clawing, lateral thrashing of the trunk, and rotating or thrashing of the tail, occurred during the initial 30 minutes (Figure 70). My hand hold had to be changed frequently during the second through fourth minutes to maintain struggling. Movement became discontinuous and considerably less forceful during minutes four through nine. Iguanas were practically helpless during inactive periods. Total activity peaked at 25 C (sum of movements per 9 minutes = 189, 324, 405, 326, 298, and 236 in Figure 70). This seems to contradict the data indicating a steadily increasing oxygen debt as T_b increased. The experiment should be repeated with a large sample, ideally with each individual exercised only once at only one T_b. Subjectively, based on the hand exercising of six iguanas, power output as well as the quickness of individual movements appeared to increase from 15 C into the preferred range.

Iguanas commonly became briefly apneustic and bloated during exercise, especially after the initial minute at T_b's of 25 C and below. Apnea occurred during the initial seconds of oxygen monitoring in four of thirty runs. The first peak in the oxygen consumption record after apnea ceased was disregarded as inaccurately high, and the second lower peak was taken as the maximum instantaneous rate during the recovery period. Unfortunately, individuals may have a still greater metabolic rate during the exercise period, when measurements were not taken. Bennett and Gleeson (1976) demonstrated that oxygen consumption in *Sceloporus occidentalis* maximized during the five minute exercise

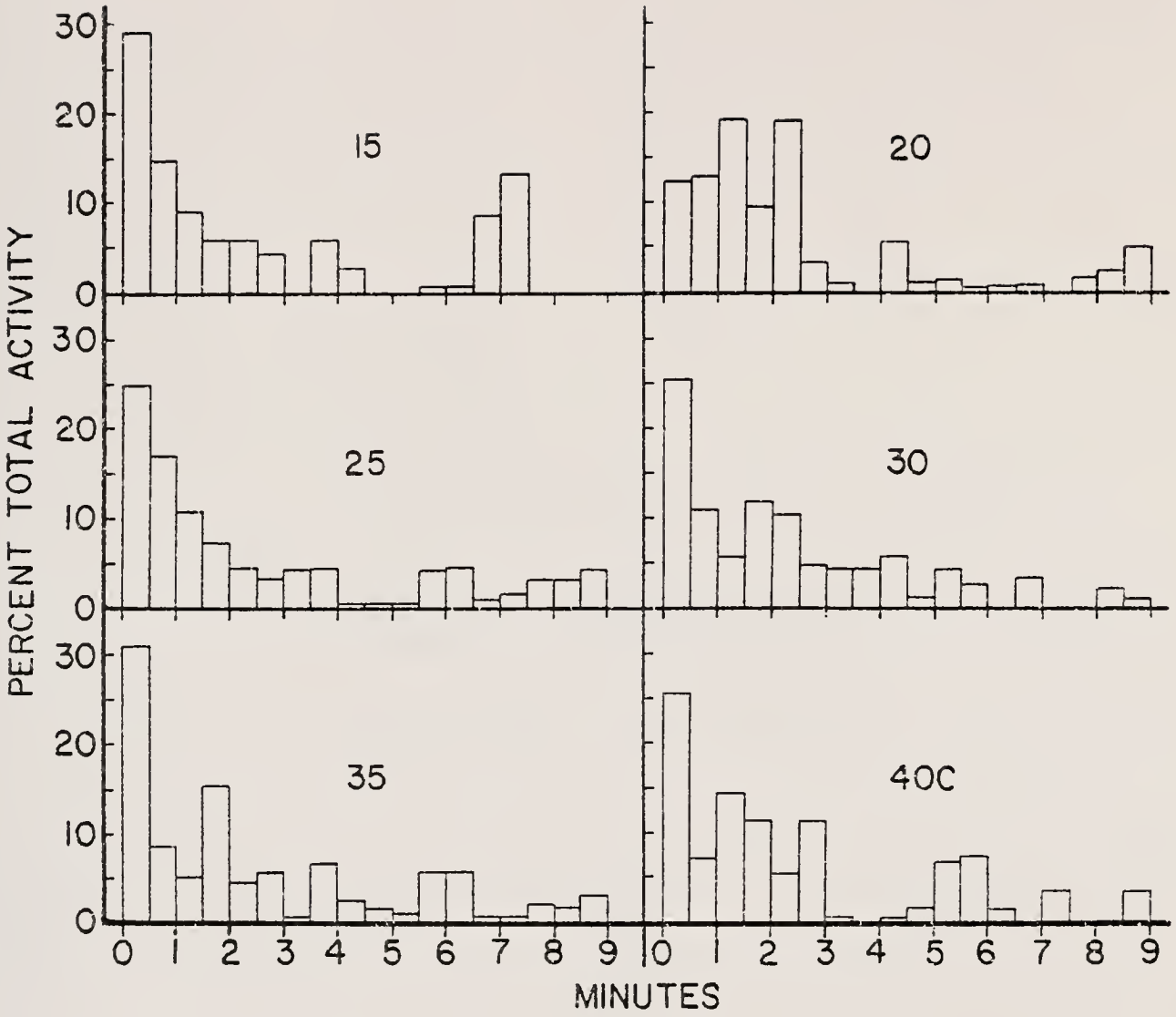


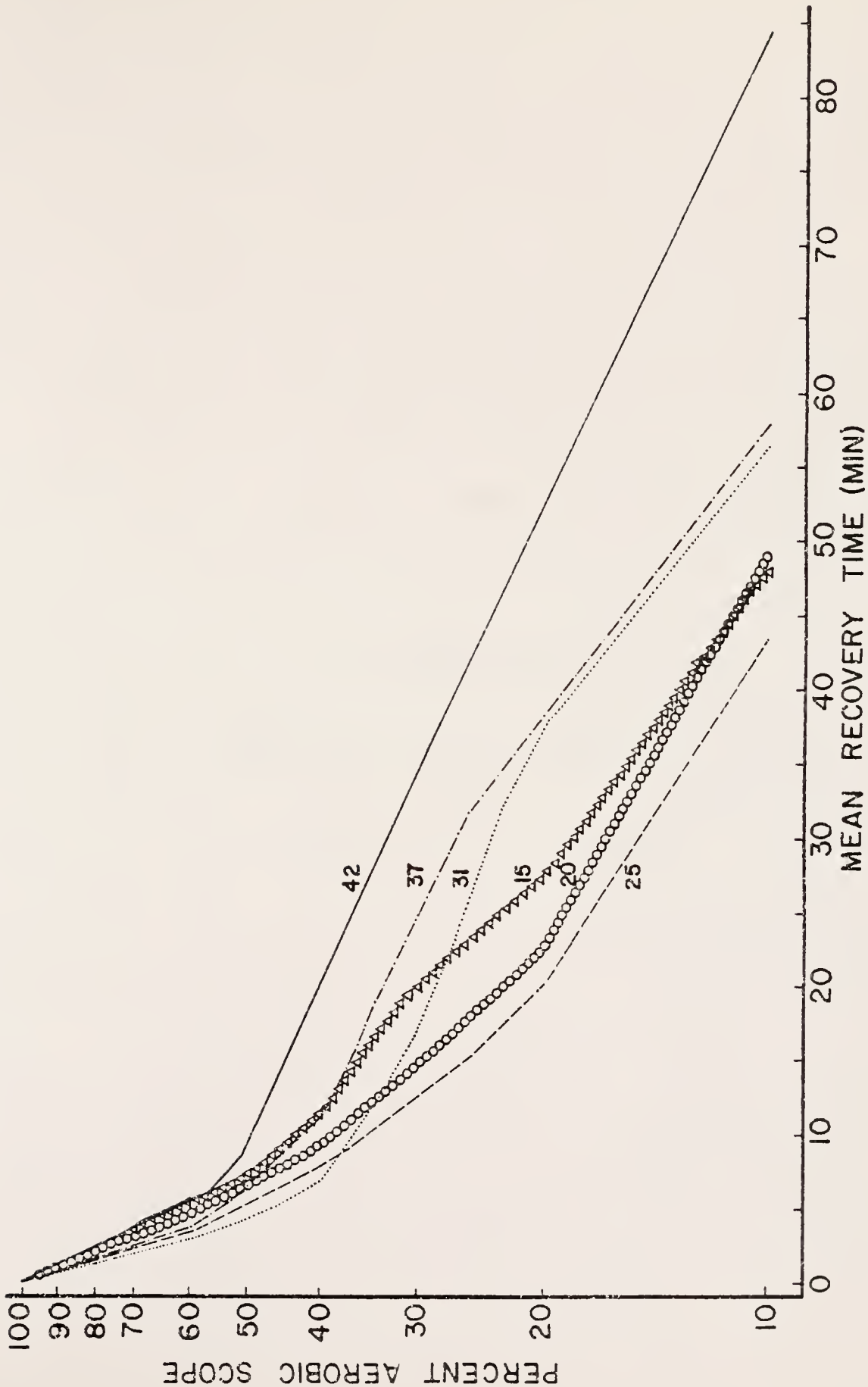
Figure 70. Temporal pattern of body movements while struggling to escape. The records are for a single 450 g male tested on six consecutive days. Each tail rotation or thrash, trunk thrash, and walking movement of opposing fore and rear legs was counted as one activity unit. Activity occurring each half minute was converted to a percentage of the total activity per nine minutes.

period at T_b's of 25 to 40 C, rather than during the subsequent recovery period.

The procedure of Bennett (1972) was used to analyze the recovery records. A smooth curve was drawn through each recovery record, necessitated by the small volume of the mask. The times required to reach 75, 60, 50, 40, 30, 25, 20, and 10 percent of each lizard's aerobic scope were taken from each of the thirty records. Sample means were calculated for each percent recovery at each T_b. The resulting recovery patterns at the six T_b's were plotted in Figure 71. Recovery was completed most rapidly at T_b's of 15-25 C, more slowly at 31-37 C, and most slowly at 42 C. Return to the resting rate of oxygen consumption obviously required a long time, an average of 89, 86, 82, 102, 99, and 118 minutes at T_b's of 15, 20, 25, 31, 37, and 42 C, respectively. The return of whole body lactate to the resting level probably required even longer. *Sauromalus hispidus* had somewhat similar recovery patterns (Bennett 1972), recovering most rapidly at 25-30 C and least rapidly at 15 and 40 C. The main difference between the results for the two species was *Cyclura*'s slower recovery at T_b's of 31 C and higher, especially in the later minutes. The standard deviation of the mean partial recovery time at each T_b increased linearly as recovery time increased. This was probably due to individual differences in recovery efficiency as well as unequal work outputs during the exercise period. The sample size was too small to test for possible sex and size related differences in recovery rates.

The rather abrupt change in the slopes of the lines in Figure 71 indicates that two or more processes with different equilibration rates were operating during recovery from exercise (Bennett 1972). The

Figure 71. Effect of body temperature on the rate of recovery from seven minutes of maximum activity. Lines were fitted by eye to mean values for five adult *Cyclura carinata*. T_b is given above each recovery curve.


PERCENT AEROBIC SCOPE
100
90
80
70
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80
MEAN RECOVERY TIME (MIN)
42
37
31
15
20
25

elimination of the alactacid debt, the more rapid process, has been equated with the replacement of oxygen stores in the blood and tissues and utilization of oxygen during the resynthesis of creatinine phosphate. The elimination of the lactacid debt corresponds to the conversion of lactic acid (Margaria *et al.* 1933). This is probably an oversimplification of the biochemistry involved (Stainsby and Barclay 1970). Nevertheless, it is still worthwhile to assume a two process recovery when analyzing the data.

The curves in Figure 69 were approximated by the equation:

$$\text{Percent Aerobic Scope} = K_1 e^{-\frac{t}{T_1}} + K_2 e^{\frac{t}{T_2}} \qquad (16)$$

where T_1 and T_2 are the time constants in minutes to 63 percent recovery of the fast (alactacid) and slow (lactacid) components, respectively, K_1 and K_2 are the intercepts of the components, t is the recovery time in minutes, and e is the base of natural logarithms (see Atkins 1969, pp. 101-106, for the method of calculation). The total oxygen debt to 95 percent recovery was estimated by summation of the areas under the curves of the log of the aerobic scope ($cm^3 O_2 \cdot kg^{-1} \cdot min^{-1}$) vs. time for the two components. The results of these calculations are given in Table 22. The alactacid debt was much smaller than the lactacid debt at all T_b's. The alactacid debt was practically independent of T_b while the lactacid debt and, thus, the total debt were highly temperature dependent. Similar results were found for *Sauromalus hispidus* (Bennett 1972). However, total recovery oxygen was greater in *Cyclura* at 31 C and above. This difference is not due to the weight differences of the lizards in the two samples ($\bar{X}$ weight = 574 and 1252 g for *Sauromalus* and *Cyclura*, respectively).

Table 22. Recovery oxygen for *Cyclura carinata* after seven minutes of maximum exercise.

	ALACTACID DEBT			LACTACID DEBT			TOTAL OXYGEN DEBT OR RECOVERY OXYGEN
Body Temperature	K_1 (% Scope)	T_1 (Min)	Debt (cm^3O_2/Kg)	K_2 (% Scope)	T_2 (min)	Debt (cm^3O_2/Kg)	(cm^3O_2/Kg)
15	35.8	1.7	2.5	64.2	25.3	32.9	35.4
20	61.6	5.5	12.7	38.4	37.9	50.1	62.8
25	57.9	3.6	11.0	42.1	30.5	74.0	85.0
31	44.5	2.1	5.8	55.5	35.1	122.5	128.3
37	43.7	1.8	5.6	56.3	33.1	170.4	176.0
42	42.8	2.2	6.6	57.2	46.3	215.7	222.3

The actual mean recovery times at various T_b's can be compared to calculated recovery times based on known mean rates of oxygen consumption (Table 23). When the iguana is assumed to be metabolizing at its maximum rate during recovery and using all its oxygen consumption in the recovery process, an obviously impossible approach, recovery is achieved an average of 6.2 times faster than actual over the T_b range of 15 to 42 C. The multiple is not much smaller ($\bar{X}$ = 4.85) when the animal is assumed to be metabolizing maximally and reserving its resting metabolism for processes other than recovery; that is, using its full oxygen scope for recovery. The portion of oxygen consumption devoted to recovery is closer to the resting rate over most of the T_b range, a mean of 1.2 times the mean resting rate from 15 to 37 C. Thus, assuming the iguana was totally quiescent during recovery in the dark, a reasonable estimate, approximately the overall equivalent of the resting metabolic rate was devoted to recovery.

Total recovery oxygen to 95 percent of the standard rate was also calculated directly by measuring the area under the curves of the recorder readouts. A plot of total recovery oxygen (cm^3O_2/kg) vs. T_b was best fitted by a second degree polynomial:

$$\text{Log Recovery Oxygen} = -0.00046\ T_b^2 + 0.0553\ T_b + 0.8449 \qquad (17)$$

$$(N = 27,\ 13.4 \leq T_b \leq 42.0,\ r = 0.946)$$

The Q_{10} for total recovery oxygen decreased from 2.58 between 15 and 16 C to 1.49 between 41 and 42 C. The mean rate of recovery [$cm^3O_2/(g \cdot hr)$/min] during the first 5 minutes vs. T_b was best fitted by the equation:

$$\text{Log Mean Recovery Rate}_1 = -0.00127\ T_b^2 + 0.0949\ T_b - 3.1627 \qquad (18)$$

$$(N = 29,\ 13.4 \leq T_b \leq 42.0,\ r = 0.787)$$

Table 23. Comparison of actual mean recovery time after maximum exercise with recovery times at three hypothetical rates of oxygen utilization.

Body Temperature	Actual Mean Recovery Time (Min)	Calculated Recovery Time (Actual ÷ Calculated)		
		Oxygen Consumption Rate: Maximum	Scope	Resting
15	89	13.1(6.8)	16.1(5.5)	70.3(1.3)
20	86	14.8(5.8)	17.8(4.8)	86.1(1.0)
25	82	13.8(5.9)	16.7(4.9)	80.5(1.0)
31	102	15.0(6.8)	18.6(5.5)	77.8(1.3)
37	99	16.9(5.9)	22.4(4.4)	68.4(1.4)
42	118	19.9(5.9)	29.8(4.0)	59.7(2.0)

The rate became practically independent of T_b near the preferred range of the lizard (Figure 72). The mean recovery rate during the latter part of the recovery period, from minute 15 to the return to the resting rate of oxygen consumption, vs. T_b was best fitted by the equation:

$$\text{Log Mean Recovery Rate}_2 = 0.0228\ T_b - 3.4725 \qquad (19)$$

$$(N = 29,\ 13.4 \leq T_b \leq 42.0,\ r = 0.805)$$

Thus, the mean rate of late recovery increased linearly with increasing T_b.

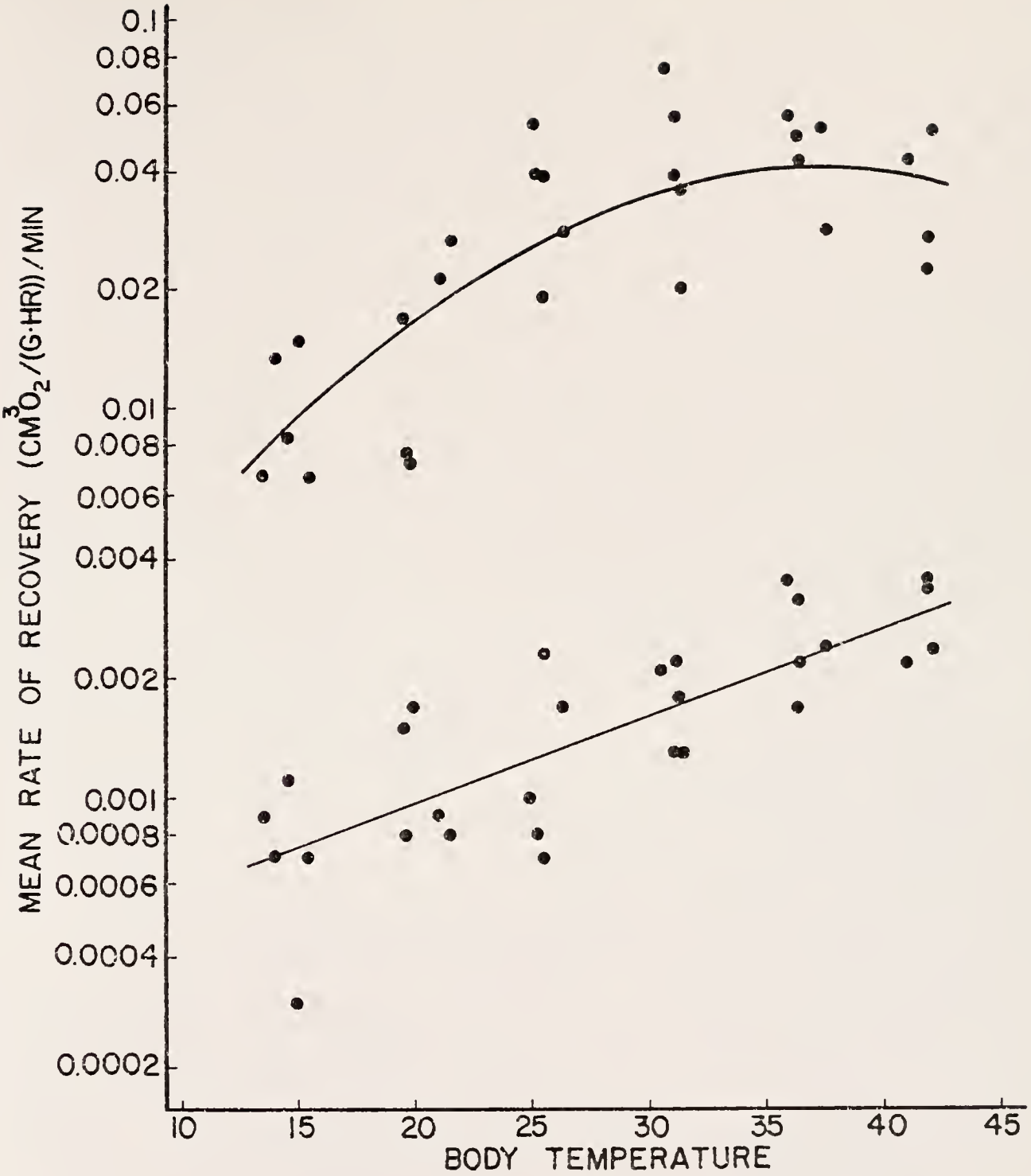


Figure 72. Early and late phase recovery from maximum exercise in *Cyclura carinata* at different body temperatures. The mean rate of change in oxygen consumption from the cessation of exercise to the end of the fifth minute of recovery (upper points) and from the fifteenth minute to the resting metabolic rate (lower points) are plotted against T_b. Curves were drawn using equations (18) and (19), respectively.

DISCUSSION

Body Temperature Relations

Comparison of *Cyclura carinata*'s Mean Body Temperature with Other Diurnal Lizards

In order to rank *Cyclura carinata* according to its relative degree of heliothermy, field body temperatures of diurnal lizards from five families have been taken from the literature and catalogued in Table 24. Unfortunately, interspecies T_b comparisons are not completely reliable, since the data were collected under a variety of conditions. T_b's were measured in different seasons. All occupied habitats may not have been sampled adequately. Some lizards may not have reached regulating phase T_b's when they were captured. Some samples may be biased by collecting too many lizards displaying a particular behavior; for example, mainly perched individuals (Licht *et al.* 1966, Bradshaw and Main 1968). Nonetheless, as the number of species for which data is available increases, the likelihood of making an incorrect statement about the relative degree of heliothermy of any one species decreases.

Cyclura has a high T_b in comparison to most other diurnally active lizards. Of the skinks, 29 of 30 species fall below *Cyclura*'s mean T_b range of 38.0-39.7 C, only one species is in the range, and none are above it (29, 1, 0). *Cyclura*'s relative standing in the other families are: iguanidae (47, 6, 1), varanidae (2, 1, 0), agamidae (5, 3, 1), teiidae (5, 1, 8), overall (89, 11, 11, or 80.2, 9.9, 9.9 percent. Only in the teiidae do the majority of the T_b's lie above *Cyclura*'s.

Table 24. Field body temperatures of diurnally active lizards. Species in each family are arranged according to increasing mean body temperature. Lizards which are herbivorous as adults are marked with an asterisk.

SPECIES	$\bar{X}$ T_B	SE	RANGE	SOURCE
		AGAMIDAE		
Moloch horridus	34.0		27.0-40.0	Pianka and Pianka 1970
Amphibolurus minimus	34.2	0.31	32.6-37.4	Bradshaw and Main 1967
Amphibolurus barbatus	34.8	0.37	30.0-39.7	Lee and Badham 1963
Amphibolurus ornatus	36.6	0.23	33.0-41.8	Bradshaw and Main 1967
Amphibolurus reticulatus	37.0	0.90	35.0-40.6	Licht *et al.* 1966
Amphibolurus isolepis	38.8	0.3	37.8-39.3	Pianka 1971b
Amphibolurus caudicinctus	39.0	0.48	34.8-41.0	Licht *et al.* 1966
Amphibolurus inermis	36.1			Pianka 1971a
	36.7	0.53	34.0-43.8	Bradshaw and Main 1967
	39.3			Licht *et al.* 1966
Diporophora bilineata (Lizards arboreally active at noon)	44.3	0.33	42.3-46.0	Bradshaw and Main 1967
		IGUANIDAE		
Anolis oculatus	27.4		21.7-32.0	Ruibal and Philobosian 1970
	28.2	0.17	23.2-33.0	Brooks 1968
Anolis limifrons	28.5	0.59	25.6-31.0	Ballinger *et al.* 1969
Anolis allogus	29.2	0.06	26.2-33.5	Ruibal 1961
Anolis lucius	29.3	0.10	24.8-32.4	Ruibal 1961
Anolis acutus	30.3		25.6-34.8	McManus and Nellis 1973
* *Basiliscus plumifrons*	31.7	0.50	28.0-35.5	Hirth 1964
Anolis homolechis	31.8	0.14	26.2-35.0	Ruibal 1961
* *Conolophus subcristatus* (Taken during intermittent overcast)	32.0		25.7-37.5	Carpenter 1969
Anolis allisoni	33.0	0.21	28.2-36.6	Ruibal 1961
Anolis sagrei	33.1	0.22	27.4-36.1	Ruibal 1961

Table 24. Continued.

SPECIES	$\bar{X}$ T_B	SE	RANGE	SOURCE
		IGUANIDAE (Continued)		
Sceloporus occidentalis	33.4	0.30	15.2-38.8	Cunningham 1966
Sceloporus merriami	33.6		29.6-37.4	Brattstrom 1965
Sceloporus gracilis	33.6		30.3-39.1	Brattstrom 1965
Sceloporus poinsetti	34.2		30.8-38.4	Brattstrom 1965
Phrynosoma solare	34.7			Baharav 1971
Basiliscus vittatus	34.7	0.07	32.6-36.5	Hirth 1964
Uta thalassina	34.8	0.40	32.6-38.5	Soule 1963
Sceloporus magister	34.8	0.17		Parker and Pianka 1973
Sceloporus undulatus	34.8		25.0-38.9	Brattstrom 1965
Phrynosoma coronatum	34.2	0.69	20.8-40.6	Cunningham 1966
	34.9		28.0-43.0	Heath 1965
Sceloporus jarrovi	35.0		32.2-37.0	Brattstrom 1965
Urosaurus nigricaudus	35.0	0.51	33.8-39.5	Soule 1963
* *Conolophus pallidus*	35.1		31.6-37.1	Carpenter 1969
Sceloporus graciosus	35.2	0.24	22.7-39.2	Cunningham 1966
Sceloporus squamosus	35.3		32.5-38.0	Brattstrom 1965
* *Cyclura pinguis*	35.3		27.1-39.8	Carey 1975
Urosaurus ornatus	35.5		26.8-39.5	Brattstrom 1965
Sator grandaevus	35.5	0.42	30.2-39.5	Soule 1963
Holbrookia maculata	35.7		40.8	Clark 1965
Sceloporus orcutti	35.9	0.32	32.6-38.5	Soule 1963
Sceloporus olivacea	36.0			Brattstrom 1965
Urosaurus graciosus	36.1	0.26		Pianka and Pianka 1970
* *Iguana iguana*	36.1		34.0-37.2	Hirth 1963
	36.1		42.4	McGinnis and Brown 1966
Uta stansburiana	35.0	0.29	20.9-40.6	Cunningham 1966
	36.2	0.24	32.1-39.8	Soule 1963
Sceloporus woodi	36.2	0.25		Bogert 1949a
Urosaurus auriculatus	36.3		32.3-39.0	Brattstrom 1965
Urosaurus clarionensis	36.4		29.6-39.0	Brattstrom 1965
* *Cyclura cornuta stejnegeri*	36.8		35.8-37.8	Wiewandt 1977

Table 24. Continued.

SPECIES	$\bar{X}$ T_B	SE	RANGE	SOURCE
		IGUANIDAE (Continued)		
Phrynosoma platyrhinos	36.8		29.0-43.0	Heath 1965
Sceloporus varibilis	36.9		33.6-40.0	Brattstrom 1965
* *Ctenosaura hemilopha*	37.1	0.53	32.0-39.6	Soule 1963
* *Ctenosaura similis*	37.1		34.5-40.1	Fitch 1973
Crotaphytus collaris	37.2		20.7-43.3	Brattstrom 1965
Uma scoparia	37.3	0.40		Pianka and Pianka 1970
* *Sauromalus obesus*	35.3		41.9	Johnson 1965
	37.7		42.0	Cowles and Bogert 1944
			46.0	Case 1976
* *Amblyrhynchus cristatus*	32.5	0.57	26.7-37.5	Bartholomew 1966
(Lizards in the prostrate basking posture)				
	37.9	0.33	36.2-40.0	Bartholomew 1966
(Lizards in the elevated basking posture)				
Holbrookia propinqua	37.9		40.9	Judd 1975
Holbrookia lacerata	38.1		42.5	Clark 1965
Phrynosoma m'calli	38.3		43.0	Heath 1965
* *Uromastix acanthinurus*	38.0-39.5		21.0-46.0	Grenot 1976
Uma notata	38.8		35.0-40.5	Cowles and Bogert 1944
* *Cyclura carinata*	38.0-39.7		33.7-42.5	Present study
(Free-ranging lizards only)				
Crotaphytus wislizeni	39.2	0.32	36.5-41.8	Cummingham 1966
Callisaurus draconoides	38.6	0.24	34.6-41.4	Soule 1963
	39.4	0.76	36.4-42.4	Cunningham 1966
* *Dipsosaurus dorsalis*	40.9	0.44	34.0-43.6	Cunningham 1966
	42.1		38.0-46.4	Norris 1953
		SCINCIDAE		
Eumeces anthracinus	25.0		13.9-33.0	Brattstrom 1965
Eumeces skiltonianus	25.0	1.36	16.8-34.0	Cunningham 1966
Sphenomorphus sabanus	25.8		24.0-28.4	Brattstrom 1965
Eumeces gilberti	26.7		21.5-31.0	Brattstrom 1965
Eumeces brevilineatus	28.0			Brattstrom 1965

Table 24. Continued.

SPECIES	$\bar{X}$ T_B	SE	RANGE	SOURCE
		SCINCIDAE (Continued)		
Lygosoma septentrionalis	28.5		24.4-32.0	Brattstrom 1965
Lygosoma laterale	28.8		22.0-35.5	Brattstrom 1965
Leiolopisma rhomboidalis	28.9	0.58	24.2-35.0	Wilhoft 1961
Eumeces laticeps	29.3		22.8-33.2	Brattstrom 1965
Sphenomorphus tympanum	29.4		18.2-36.5	Spellerberg 1972c
Sphenomorphus quoyi	30.0		17.4-34.2	Spellerberg 1972c
Ctenotus brooksi	30.6	0.36		Pianka 1969
Leiolopisma fuscum	30.8	0.32	24.5-34.5	Wilhoft 1961
Sphenomorphus kosciuskoi	30.9		16.9-36.0	Spellerberg 1972c
Ctenotus dux	32.0	0.35		Pianka 1969
Tiliqua scincoides	32.6		39.5	Bartholomew *et al.* 1965
Tiliqua rugosa	32.7		27.0-36.5	Licht *et al.* 1965
Mabuya rudis	32.8		25.4-38.6	Brattstrom 1965
Ctenotus helenae	32.8	0.52		Pianka 1969
Eumeces fasciatus	33.0		13.5-37.0	Brattstrom 1965
Mabuya mabouia	33.0	0.43	30.1-37.7	Brooks 1968
Ctenotus pantherinus	33.1	0.38		Pianka 1969
Ctenotus schomburgkii	33.3	0.39		Pianka 1969
Eumeces obsoletus	34.0		17.5-36.3	Brattstrom 1965
Ctenotus grandis	34.2	0.51		Pianka 1969
Ctenotus atlas	34.5	0.83		Pianka 1969
Ctenotus calurus	35.6	0.36		Pianka 1969
Ctenotus quattuordecimlineatus	35.8	0.30		Pianka 1969
Mabuya striata	35.8		31.0-39.5	Brattstrom 1965
Ctenotus leae	37.7	0.41		Pianka 1969
Ctenotus leonhardii	38.0	0.20		Pianka 1969
		TEIIDAE		
Ameiva fuscata	36.1	0.28	26.0-40.1	Brooks 1968
Ameiva festiva	36.2	0.26	32.0-39.8	Hirth 1964
Ameiva ameiva	37.6		35.1-39.3	Brattstrom 1965

Table 24. Continued

SPECIES	$\bar{X}$ T_B	SE	RANGE	SOURCE
		TEIIDAE (Continued)		
Ameiva quadrilineata	37.6	0.06	34.6-40.0	Hirth 1964
Ameiva pluvianotata	37.8	0.34	33.8-40.0	Hirth 1964
Cnemidophorus lemniscatus	38.8		34.5-42.3	Brattstrom 1965
Cnemidophorus hyperythrus	39.9	0.25	38.3-41.6	Soule 1963
Cnemidophorus exsanguis	39.9	0.16		Schall 1977
Cnemidophorus ceralbensis	40.0	0.45	37.4-42.5	Soule 1963
Cnemidophorus inornatus	40.2	0.10		Schall 1977
Cnemidophorus gularis	40.2	0.16		Schall 1977
Cnemidophorus tigris	39.4	0.38	20.0-44.6	Cunningham 1966
	40.4	0.09		Schall 1977
Cnemidophorus sexlineatus	41.0	0.47	38.5-43.0	Bogert 1949
Cnemidophorus tessellatus	40.1	0.13		Schall 1977
	41.3	0.24	37.4-43.5	Bogert 1949b
		VARANIDAE		
Varanus varius	35.5		35.0-36.2	Stebbins and Barwick 1968
Varanus gouldii	37.1	0.76	34.4-36.2	Licht *et al.* 1966
Varanus komodoensis	38.1		36.0-40.0	McNab and Auffenberg 1976

Do herbivorous lizards require higher T_b's to digest their food? Janzen (1973) has suggested that the teiids, *Ameiva ameiva* and *Cnemidophorus lemniscatus*, insectivorous on the mainland of Costa Rica and primarily fruit and vegetation eaters on the island of Providencia, have elevated their T_b on the island as a result of the difference in diet. The island lizards "must maintain the internal compost heap at a high temperature in order to process foliage fast enough to get the energy needed." Janzen made no T_b measurements of mainland and island forms, however, only stating that island forms basked more frequently. The data in Table 24 are also suggestive. The mean active T_b for 23 genera of primarily carnivorous lizards from four families is 34.8 C ($\bar{X}$ + 2 SE = 36.1 C), lower but not significantly lower than the mean for nine genera of herbivorous iguanids, 36.8 C ($\bar{X}$ + 2 SE = 37.3). Apparent or gross digestive efficiency is probably significantly lower in herbivorous than in carnivorous lizards, especially when leaf vs. insect eaters are compared (Shine 1971, Iverson 1977). The digestive efficiency for fruits and flowers, with their lower fiber content, is probably higher than for leaves, at least in *Cyclura* (Auffenberg, in prep.). Both *Cyclura stejnegeri* (Wiewandt 1977) and *Cyclura carinata* prefer fruits to leaves in the field.

Digestive efficiency improves as the preferred T_b is reached in *Dipsosaurus dorsalis* (Harlow *et al.* 1976). A higher field T_b, as expressed during a long basking period, may compensate for the lower digestibility of foliage. However, it is premature to state this absolutely.

Seasonal Variation in Body Temperatures of Active Lizards

As available ambient temperatures and radiant heat input gradually decline in the fall of the year, diurnal heliothermic lizards must do at

least one of three things: 1) spend a greater proportion of their day basking rather than foraging, etc., 2) lower their T_b during activity, or 3) brumate. Heliotherms in the subtropics and tropics do not brumate while temperate species do, such as *Dipsosaurus dorsalis* and *Sauromalus obesus*. Seasonal mean T_b ranges of active lizards which do not brumate, 3.4 C in *Amphibolurus isolepis* (tropical Western Australia, Pianka 1971b), 5.5 C in *Sceloporus occidentalis* (Berkeley, Calif., Mayhew 1963), may usually be greater than for active lizards that do brumate; for example, 2.5 C in *Amphibolurus fordi* (New South Wales, Australia, Cogger 1974). The *Cyclura carinata* range was only 0.5 C at Site II for February to October. However, December-January MBT's for active lizards probably fell below 38.9 C. The MBT of *Cyclura cychlura figginsi*, measured in January between 1000 and 1400 on Great Exuma in the Bahamas approximately 120 miles north of Water Cay, averaged only 31.4 C (Windrow 1977). However, some of Windrow's values may have been obtained from lizards in the morning heating phase. One clear indication that *C. carinata* becomes more eurythermal in the winter is the significantly lower mean February T_b at the start of foraging. Based on the thermal gradient results, the seasonal lowering of the MBT is probably not due to a decline in the preferred T_b, caused by thermal acclimatization or shorter photoperiod. However, a reduced winter food supply, resulting in a lowered intake, may be partially responsible for any MBT decline.

Stability of the Mean Preferred Body Temperature

The stability of the MPT varies in different lizard species. However, insufficient data are available to determine whether temperate species have less stable MPT's than tropical species.

To test for seasonal acclimatization stability of the MPT, lizards are collected from the field at regular intervals and tested immediately in a photothermal gradient. McGinnis (1966) found no change in the MPT of *Sceloporus occidentalis* using this technique. March and September results for *Anolis carolinensis* were not significantly different (Licht 1968). In the present study, winter and summer samples of *Cyclura carinata* had about the same MPT's. On the contrary, the MPT in *Sauromalus obesus* varied by more than 2.5 C during a 2 year period, with no logical pattern to the variation (Case 1976). *Lacerta vivipara* MPT's, measured in southern England, varied by 5.1 C between April and October (Patterson and Davies 1978).

The commonly used technique to determine acclimation stability of the MPT is to collect a single sample, divide it into several groups, keep each group at a different acclimation temperature in a controlled environmental chamber for at least 2 weeks, and then test individuals in a photothermal gradient. Results from different species are inconsistent, as are the seasonal acclimatization results. *Eumeces laticeps* had equal MPT's after acclimation at 14, 22, and 28 C (Pentecost 1974). Other workers have reported inverse acclimations; Wilhoft and Anderson (*Sceloporus occidentalis* 1960) and Mueller (*S. occidentalis* and the California sample of *S. graciosus* 1970) found a lowering of the MPT in their 35 C groups. The responses may have been pathological, since 35 C is above the mean T_b of the field caught lizards. Licht (1967) found a slightly lower MPT in *Anolis* acclimated at 32 C than at 20 C. The difference was significant only during the second of three days in the gradient. Mueller (1970) reported a higher MPT in the 15 C

acclimation group than in the 25 and 35 C groups of Wyoming caught *Sceloporus graciosus*.

Even if the MPT is fairly stable over a wide range of acclimation temperatures, thermoregulatory precision is commonly greater after low temperature acclimation. McGinnis's winter *Sceloporus* sample had a narrower T_b range than his summer sample (31.7-37.3 vs. 28.6-38.7 C, respectively). The same was demonstrated for *Cyclura* in the present study. Pentecost's *Eumeces* acclimated to 14 C did not reach T_b's as high as lizards in the 22 and 28 C groups (38.3 vs. 42.8 and 40.7 C, respectively). In accord with these results, low temperature acclimation decreases the critical thermal maximum in lizards (Lowe and Vance 1955; Ballinger and Schrank 1970, Corn 1971).

Late Afternoon Maximum Body Temperature

Adult male and female *Cyclura* spent considerable time in the vicinity of the nocturnal retreat after completion of the final foray. The post-foray period averaged 97 minutes in February (SD = 61, Range = 17-191, N = 11 days) and 86 minutes in October (SD = 41, Range = 12-140, N = 10 days) and started at a mean time of 1449 (Range = 1336-1548) and 1416 (Range = 1312-1530), respectively. Much of this time was spent basking in one spot and often led to the highest T_b recorded during the day, especially during the hot summer months. The highest maximum voluntary tolerance, 43.8 C, was recorded during this time, a temperature above the panting thresholds determined earlier in the day, indicating an increased late afternoon high temperature tolerance. Lizards commonly selected the same wind protected location night after night and always assumed the prostrate basking posture. Dorsal cutaneous vasodilation and

ventral cutaneous vasoconstriction were likely during this time (White 1973).

The morning and afternoon T_b's of many small lizard species are not significantly different: *Anolis cristatellus* (Huey 1974), *Amphibolurus barbatus* (Lee and Badham 1963), *Amphibolurus inermis* (Heatwole 1970), *Cnemidophorus hyperythrus* (Bostic 1966), *Holbrookia propinqua* (Judd 1975), and *Sceloporus orcutti* (Mayhew 1963). All five tropical *Anolis* species examined by Ruibal (1961) had significantly higher afternoon T_b's. This may have been due to higher afternoon air temperatures, as he suggested, or to including morning heating phase records in the morning sample.

Reptiles reported to maximize T_b late in the afternoon are all large: *Conolophus subcristatus* (Werner, D., personal communication), *Geochelone elephantopus* (Mackay 1964), *Sauromalus obesus* (Case 1976), *Varanus komodoensis* (McNab and Auffenberg 1976), and *Varanus varius* (Stebbins and Barwick 1968). These reports are all based on small sample sizes, however. Late afternoon T_b maxima are probably more common in large reptiles due to the physics of heat exchange. Of course, the lizard must also voluntarily tolerate high afternoon T_b's. Daily late afternoon T_b maxima have also been reported in a number of large mammals; camel (Schmidt-Nielsen *et al.* 1957), camel, giraffe, water buffalo, eland, oryx, and Ankole steers (Bligh and Harthoorn 1965), and euro, gray and red kangaroos (Brown and Dawson 1977).

The late afternoon maximum T_b may be an example of temperature hardening, defined by Precht (1973) as "a quick, usually transitory, adaptation to high and low temperatures." Earlier exposure to high temperatures during the day may have resulted in a short term increase

in heat tolerance, lost during the subsequent night. Heat hardening (see Hutchison and Maness 1978 for a review) is not the same as acclimatization, a longer lasting response to temperatures in the normal range. Strictly speaking, the iguanas had not been heat hardened, since T_b was always below the CTMax. However, Hutchison and Maness' definition may be found to be too restrictive when the bicchemical basis of the phenomenon is finally determined. Of course, a circadian cycle of temperature tolerance may also be involved. However, this possibility was not investigated in the present study.

Thermal Safety Margins

Heatwole (1970) defined six thermal safety margins: 1) PTSM-CTM, a physiological thermal safety margin; the difference between the critical thermal maximum and the mean T_b in a thermal gradient, 2) PTSM-LM, a physiological thermal safety margin; the difference between the lethal maximum and the mean T_b in a thermal gradient, 3) ETSM-CTM, an ecological thermal safety margin; the difference between the CTM and the mean regulating phase, field T_b, 4) ETSM-LM, another ecological thermal safety margin; the difference between the LM and the mean regulating phase, field T_b, 5) MTSM-CTM, a minimum thermal safety margin; the difference between the CTM and the maximum field T_b, and 6) MTSM-LM, another minimum thermal safety margin; the difference between the LM and the maximum field T_b. The values for *Cyclura* are: PTSM-CTM, 9.2 C; PTSM-LM, 11.0; ETSM-CTM, 6.3 and 8.1 (June and July); ETSM-LM, 8.3 and 9.9; MTSM-CTM, 3.7 and 5.5; MTSM-LM, 5.5 and 7.3. These values are slightly smaller than for the majority of the 39 species of lizards listed by Heatwole; that is, 61 margins are larger, 38 are in

range, and only 14 are smaller. This is further evidence that *Cyclura* maximizes its field T_b's in the summer. Heatwole suggested that this is possible in tropical species due to the predictable nonvarying nature of the upper limit of environmental temperatures.

Panting Threshold

The factors influencing the level of the panting threshold have been studied intensively by Heatwole and his coworkers (Chong *et al.* 1973, Heatwole *et al.* 1973, Heatwole *et al.* 1975). They found the threshold to be quite plastic. It has a diel cycle corresponding to the daily rhythm of environmental temperature. Seasonal variation is expressed as higher summer values than at other times of the year, related both to higher summer acclimatization temperature and longer photoperiod. The immediate past thermal history of the lizard affects the threshold, that is, repeated heatings to panting depressed the T_b value. Lastly, they found that random day to day individual variation, independent of environmental temperatures, is quite important.

The T_b range for the panting threshold in *Cyclura carinata* was larger than any listed by Heatwole *et al.* (Table 1, 1973). The only value approaching 11 C was that for *Amphibolurus barbatus* (31.5-42.4 or 10.7 C). One probable reason for this difference is the common use of a low heating rate for the determination of the panting threshold, which prevents unequal heat distribution in the reptile's body. Templeton (1971) increased the panting threshold of *Dipsosaurus dorsalis* from 39.0 to 43.5 C by decreasing the heating rate. However, rapid heating of *Amphibolurus muricatus* did not depress the panting threshold, though it did increase the variability of the results (Heatwole *et al.*

1973). This probably was due to heat damage, since eight of ten lizards in their sample failed to recover. The *A. muricatus* threshold decreased as much as 1.3 C during ten consecutive heatings of a single individual over a period of 3 hours. The same phenomenon may have occurred in the *Cyclura carinata* results illustrated in Figure 57, although the threshold would presumably not have risen again in the afternoon.

The most likely explanation for the midday depression of head and body panting threshold temperatures is the importance of a skin temperature sensory input, as demonstrated in *Sauromalus obesus* by Crawford and Barber (1974). The stomach temperature at the panting threshold in *Varanus albigularis* ranged from 35.4 to 38.6 C, whereas skin temperature remained near 39 C (Bligh *et al.* 1976), indicating that the latter was being regulated. Since the skin-core temperature difference is greatest during midday heating, the core T_b depression in *Cyclura* would be explained if skin temperature is also of major importance in the control of the panting threshold.

It should be standard procedure to find the maximum panting threshold range for each lizard species, as Spellerberg (1972a) suggested for the CTMin, since some interesting ecological correlates would be expected. This demands acclimation of lizards to a wide range of ambient temperatures prior to testing, as well as immediate testing of acclimatized lizards. A desert dwelling lizard might have a wider panting threshold range, an adaptation to both large temperature extremes and low water availability. *Amphibolurus barbatus*, occupying both arid and mesic habitats, did elevate its panting threshold in response to dehydration, adaptive as a water conserving measure in hot dry weather.

On the other hand, *A. muricatus*, a dweller of more mesic regions, did not alter its threshold T_b with increasing dehydration (Parmenter and Heatwole 1975). Secondly, maximum panting threshold ranges of heliotherms may be greater than for thigmotherms and nocturnal lizard species, which are subjected to less rapid heating and cooling rates. Thirdly, the threshold range might be expected to rise ontogenetically in species with large adult size, due to increasing temperature differences between the skin and the body core with increasing body weight.

Body Temperature and Reproductive State

Reproductively active, ovoviviparous, female snakes appear to have higher preferred field T_b's during activity than males and reproductively quiescent females. Mean T_b's of *Crotalus viridis* females were 2.1 and 2.0 C above males in the spring and summer, respectively (Hirth and King 1969). The T_b's of two oviparous species, *Masticophis taeniatus* and *Coluber constrictor*, did not differ significantly with sex. Pregnant *Thamnophis sirtalis* and *Thamnophis ordinoides* both had higher mean T_b's than males (2.3 and 2.2 C, respectively) and nonpregnant females (0.6 and 1.0 C) in a thermal gradient (Stewart 1965). Pregnant field caught female *Agkistrodon contortrix* had higher activity T_b's than males (Fitch 1960). An oviparous female *Python molurus bivittatus* elevated its T_b an average of 6.2 C (Range 4.1-7.4) above substrate temperature during brooding (Van Mierop and Barnard 1976). Also, T_b was higher above substrate temperature in the gravid snake ($\bar{X}$ = 3.1, Range 1.5-5.5) than in the same snake when postbrooding ($\bar{X}$ = 1.1 C, Range 0.1-1.7).

The pattern may be reversed in ovoviviparous and at least some oviparous lizards. Males and preovulatory and postparturient females of

Sceloporus cyanogenys and ovoviviparous species, all had higher T_b's than pregnant females in a thermal gradient (Garrick 1974). Pregnant ovoviviparous female *Lacerta vivipara* had lowered preferred T_b's in a thermal gradient than males (Patterson and Davies 1975). Gravid females of five species of oviparous *Cnemidophorus* all had lower mean T_b's than males and nongravid females, though the differences were not significant (Schall 1977). Gravid *Cyclura carinata* appear to have depressed regulating phase T_b's. Mayhew (1963), Bostic (1966), Brooks (1968), and Heatwole (1970) found no significant difference in mean T_b's of males and females of six oviparous lizard species. However, none of these workers examined the reproductive state of the females in their samples. This is necessary since all mature females may not reproduce in a given year, as Nagy (1973) found for *Sauromalus obesus*, and the period of gravid female hypothermia may be of short duration.

In the snakes, the elevated embryo temperature may prevent abnormal development (Fox *et al.* 1961) and certainly increases the rate of normal development. In the lizards, oviducal embryos are presumably more sensitive to high temperatures than the tissues of the parents.

Ethological Considerations

Lizard Activity

Cyclura is closer to a Type I than a Type II lizard (Heatwole *et al.* 1969); strictly diurnal, emergent only when T_b rises above burrow temperature, and rather stenothermal when weather permits. *Cyclura* tailors its activity period to the yearly change in photoperiod, emerging, on the average, 3 hours after sunrise and submerging an hour and a

half before sunset, regardless of season. Few forced submergences resulted from overcast, due to the usual short duration of the overcast periods and the low cooling rate of lizards due to large body size. Forced submergences due to high environmental temperatures were also rare in well vegetated areas.

Many small, burrow utilizing, diurnal heliotherms, presumably as a result of their rapid heating rates or greater eurythermality, emerge earlier than *Cyclura* during warm weather. Preemergence summer basking of *Amphibolurus fordi* in *Triodia* grass tussocks began very soon after sunrise and postemergent basking outside the tussocks started around 0715 (Cogger 1974). *Uma* sp. emerged as early as 0500 in July (Mayhew 1964), and *Amphibolurus inermis* started emerging around 0700 in summer (Bradshaw and Main 1967). *Dipsosaurus dorsalis* may be a unique case; it becomes active in its burrow up to two hours before emergence (DeWitt 1963, Gelderloos 1976), moving to the shallow portion of the burrow where it heats to the minimum voluntary tolerance of the regulating phase (McGinnis and Dickson 1967). It emerges late in the day compared to other desert lizards (Norris 1953). Type II lizards, such as many *Anolis* species, remain above ground all night and become active almost at sunrise. For example, many *Amblyrhynchus cristatus* had already finished basking and were ready to enter the sea by 0730-0800 (Carpenter 1966). However, not all diurnal lizards emerge early in the morning. As size increased in thirteen species of *Ctenotus*, some of which were sympatric, activity patterns changed in a distinct fashion (Pianka 1969). The smallest lizard group, consisting of four species, had short, midday-encompassing activity periods. The next largest group, also

consisting of four species, had longer bimodal activity distributions. Only the five largest species were active all day.

Diurnal lizards usually have a single activity peak. Unfortunately, the quantitative measure of activity is usually a tally of how many lizards are seen or captured per hour, rather than of individual lizard movement. The activity peak most commonly occurs sometimes during the morning hours during warm weather (Heath 1965, Johnson 1965, Tanner and Krogh 1974, Gelderloos 1976, present study). A morning activity peak seems adaptive on several grounds: 1) it occurs before the surface environment becomes too hot, 2) feeding is completed as soon as possible, leaving the rest of the high T_b time for digestion, 3) territorial encounters, if any, would be energetically wasteful to continue throughout the day. High environmental temperatures commonly result in a bimodal activity distribution. The daily maximum activity peak sometimes occurs in the late afternoon rather than during the morning under these conditions (*Uta stansburiana*, Irwin 1965; *Sauromalus obesus*, Nagy 1973 and Case 1976; *Gopherus berlandieri*, Rose and Judd 1975).

Cyclura remains emergent during the full time environmental temperatures are suitable for maintaining preferred T_b even during the dry season. *Dipsosaurus dorsalis*, on the contrary, does not reemerge during summer afternoons, even though environmental temperatures are suitable for it to do so. Norris (1953) and Porter *et al.* (1973) have suggested that this lack of afternoon activity is a water conserving measure. Water loss is undoubtedly less of a problem for *Cyclura* than for *Dipsosaurus*. Rain may not fall for more than 15 months in parts of the range of *Dipsosaurus*, whereas rainless months in the Caicos are rare. Also, the dry season in the Caicos is cool to warm, rather than

hot as in North American deserts. Thirdly, *Cyclura* probably has the same passive means of reducing respiratory water loss as *Dipsosaurus* (Murrish and Schmidt-Nielsen 1970); a portion of the water vapor added to the inspiratory air by evaporation is recovered by condensation on the cool nasal passages during exhalation. Fourthly, since it possesses a nasal salt gland, *Cyclura* probably also decreases water loss during the dry season by cloacal water resorption from the urine (Schmidt-Nielsen *et al.* 1963).

Eurythermy vs. Stenothermy

Eurythermic lizards spend little or no time thermoregulating. Since T_b and shaded air temperature are very similar, eurytherms are sometimes referred to as thermoconformers or as thermal generalists. Examples are most commonly found in heavily shaded, tropical forest regions: *Spenomorphus sabanus* (Inger 1959), *Anolis oculatus* (Ruibal and Philobosian 1970), *Anolis tropidolepis* (Fitch 1972), and *Anolis polylepis* (Hertz 1974). Other eurythermic lizards are slightly less air and substrate temperature dependent, occurring in more open areas: *Gerrhonotus multicarinatus* (Cunningham 1966) and *Phrynosoma platyrhinos* (Pianka and Parker 1975). Stenothermic lizards thermoregulate, maintaining T_b in a narrow range during the day in the face of changing environmental temperatures. These thermal specialists constitute the bulk of the diurnal lizard fauna in Australian, North American, and southern African deserts.

Large body size and the nature of the Caicos Island environment probably restrict *Cyclura* to a semiarboreal herbivorous niche. Due to its large body size and the low prey density, it is unlikely that adult

Cyclura could survive on a diet of insects. The three small, diurnally active lizard species present are all insectivorous; *Mabuya mabouya*, occupying the shaded leaf litter habitat; *Anolis scriptus*, occupying the shaded arboreal habitat, and *Liocephalus psammodromus*, living on the ground and preferring more open areas than *Mabuya*. *Liocephalus* has only a slightly lower activity temperature than *Cyclura* ($\bar{X}$ T_b = 36.4 C, range = 35.1-38.0, N = 15 September captures). The nearly totally herbivorous diet of even hatchling *Cyclura* (Iverson 1979) may be due to competitive exclusion by the three insectivorous species. The height and density of the Caicos vegetation are too low in most areas for *Cyclura* to be as arboreal as *Iguana iguana*. Due to its dependence on anaerobic metabolism during maximum activity and the resulting rapid onset of fatigue, it is doubtful that *Cyclura* could subdue a mammal much larger than a rat. But mammals have been absent from the Caicos until very recently. Although several species of small birds are present, it is questionable how effective iguanas would be in an arboreal pursuit. Although certainly effective for feeding on leaves and fruit, their locomotion through bushes is generally slow and rather halting. It is surprising that *Cyclura* does not feed on the smaller lizard species, especially since infrequent cannabalism has been documented (Iverson 1979). Clearly, the largest source of easily obtainable food consists of the leaves and fruits lying on the ground. Apparently, this source is insufficient or lacking in some way, as iguanas frequently secure arboreally collected fruits and leaves as well. It should be noted here that all of the largest agamids, iguanids, and scincids are herbivorous. The argument given above is essentially the same as that of Pough (1973) to explain the general phenomenon. Large teiids and

varanids may all be carnivorous due to the greater ability of these family members to sustain lengthy strenuous activity without fatigue.

A semiarboreal herbivorous habit in a xeric habitat necessitates a high regulating phase T_b. Climbing over the tops of bushes during feeding probably results in occasional T_b maxima higher than would be encountered during exclusive ground feeding. Although large herbivores have smaller home ranges than similarly sized carnivores, a rule that probably applies to lizards as well as mammals (McNab 1963, Harestad and Bunnell 1979) and birds (Schoener 1968), *Cyclura* still usually covers considerable ground during feeding. This inevitably requires crossing open areas and stopping in high temperature shade, which in turn leads to an elevated T_b. Also, *Cyclura* usually tolerates high midday temperatures rather than cooling in its burrow.

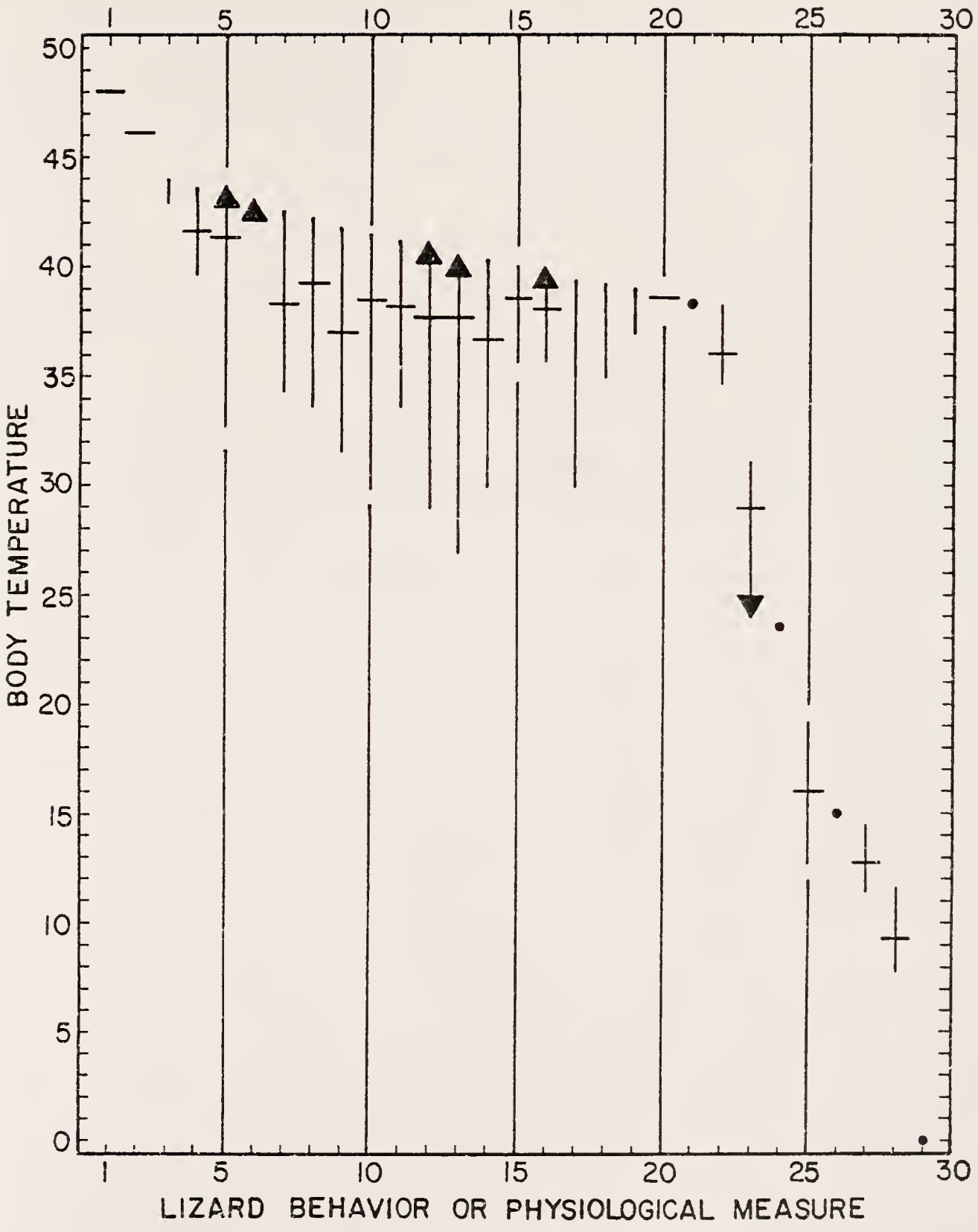
Why is *Cyclura* stenothermic? First, since the maximum upper T_b limit is less subject to change than the lower limit of the regulating phase, a high T_b lizard is forced toward stenothermia. Secondly, thermoregulation is energetically cheap in the "low cost habitats" (Huey and Slatkin 1976) occupied, fairly open vegetatively and commonly reaching high environmental temperatures. Iguanas can maintain high T_b's during mid and late summer afternoons without shuttling at all. Thirdly, food is abundantly available in sunny as well as deeply shaded areas. Lizards do not have to forage exclusively in the shade, late in the afternoon, or, as the ant eating *Phrynosoma platyrhinos* (Pianka and Parker 1975), after sunset. Since less time is devoted to feeding, more time is available for thermoregulation. Fourthly, *Cyclura* is highly territorial. Males must be able to chase other males away from their territories and females must be able to chase intruding males and

females away from their nests during the entire activity period. Keeping T_b in a narrow range as much as possible during that time is adaptive, since the lizard is physiologically more efficient over this narrow T_b range. Since enzymes function optimally within a narrow T_b range, it is energetically less expensive to function optimally only in this range, since operating optimally over a wide T_b range would require a battery of different isozymes, many of which would be inactive at any one time (Heinrich 1977).

Cyclura carinata may have some capacity for invading more densely vegetated areas, where it would be forced to maintain lower activity T_b's or become a thermoconformer. In the Gainesville pen, when the diurnal shade time increased to the point of encroaching on the minimum activity time, lizards emerged in complete shade; that is, they became more eurythermal. However, iguanas were not abundant in the Mixed Woodland habitat, an area of considerable shade. This may have been due to a lack of food or difficulty in digging burrows, rather than the high preferred T_b of the lizard. Regal (1968) maintained *Klauberina riversiana* for over a year at T_b's well below preferred with no deleterious effects on feeding or health.

Although *Cyclura* is stenothermic, it still functions adequately over the full range of T_b's normally experienced. Figure 73 illustrates most of the body temperature means and ranges measured for behaviors and physiological parameters during this study. The minimums of the T_b ranges for behaviors were more variable than the maximums (SD of $\bar{X}$ for minimums = 2.94, SD for maximums = 1.57, N = 15). This has also been noted by Hardy (1962) for *Cnemidophorus sexlineatus* and is probably common in high T_b, diurnal heliotherms. Practically the widest T_b range was

Figure 73. Summary of body temperatures of selected behaviors and physiological maxima of *Cyclura carinata*. Numbers on the abscissa refer to the following T_b's: 1) lethal maximum, 2) critical thermal maximum, 3) peak maximum oxygen consumption after strenuous exercise, 4) maximum voluntary tolerance (Feb-Oct), 5) panting threshold, 6) peak resting oxygen consumption, 7) late afternoon burrow submergence T_b in the field (Feb-Oct), 8) lizard escape attempts from June field cages, 9) preferred T_b in the thermal gradient (summer and winter samples), 10) T_b during forays (Feb-Oct), 11) clearing of nasal salt gland secretion from the nasal passages, 12) drinking (June caged field lizards), 13) defecation, 14) ground feeding (Feb, Oct), 15) arboreal feeding (Feb, Oct), 16) burrow excavation (Feb, Oct), 17) start of the first foray (Feb, Oct), 18) maximum mean recovery rate ($[cc O_2/(g \cdot h)]/min$) during the first five minutes after strenuous exercise, 19) maximum aerobic scope, 20) mean T_b of lizards in the regulating phase (Feb-Oct), 21) maximum heart rate increment, 22) minimum daily T_b of the regulating phase (Feb-Oct), 23) T_b at emergence in the field (Feb-Oct), 24) minimum observed feeding T_b in the Gainesville pen, 27) critical thermal minimum, 28) loss of eye opening ability, 29) approximate lethal minimum. Horizontal lines are means, vertical lines are ranges, and arrows indicate probable extension of the T_b range beyond the observed value.


1
5
10
15
20
25
30
50
45
40
35
30
25
20
15
10
5
0
BODY TEMPERATURE
LIZARD BEHAVIOR OR PHYSIOLOGICAL MEASURE

28.3 C for basking, extending from the minimum T_b for emergence, 15.0 C, to the maximum late afternoon T_b, 43.8 C. Thus, *Cyclura* sometimes basked at T_b's as high or higher than the ranges of many other activities, such as: drinking, defecating, foray walking, feeding on the ground and in trees, excavating burrows, and so on. This phenomenon has also been noted for *Sceloporus cyanogenys* (Greenberg 1976), presumably in individuals which were not hyperthermic during testing. Some behaviors had T_b frequency distributions which were skewed to the left: the panting threshold, escape attempts from the June cages, drinking, defecation, arboreal feeding, and emergence in the field. Skew to the right was uncommon. The likelihood of submergence into the burrow when scared, oviposition, and the minimum daily regulating phase T_b were examples.

It is adaptive for *Cyclura carinata* to maximize food intake in the preferred T_b range. Firstly, lizards were probably better equipped sensorily to find food. Campbell (1969) and Werner (1972) demonstrated fairly conclusively that hearing improved in the preferred T_b ranges of many lizard species. *Cnemidophorus sexlineatus* was more likely to lose a pursued insect that stopped moving when at a T_b of 32 C than at 40 C, presumably due to poorer sensory perception at the lower temperature (Hardy 1962). Iverson (1977) and I repeatedly observed iguanas running toward a thrown object, in an "investigative charge," a response which could be illicited by sound alone. Sites of abundant fruit drop were probably commonly found by a combination of vision, audition, and olfaction. Secondly, lizards may have remembered the location of rich food sources better when they were found while the animals were in the preferred T_b range. Lizards commonly returned to these food sources for several days in a row. *Dipsosaurus dorsalis* could learn a Y maze at T_b's of 27 and

32 C, but not at 22 C (Krekorian *et al.* 1968). Unfortunately, due to using a heat source as a reinforcement, no testing was done in the lizard's preferred range. Thirdly, reptiles commonly are more efficient locomotorily when in their preferred T_b ranges. Cruising rate was independent of T_b in the preferred range in *Thamnophis sirtalis* (Heckrotte 1967) and *Cyclura*. The same was true for gross activity in *Amphibolurus barbatus* (Lee and Badham 1963). Arboreal feeding was undoubtedly more energetically demanding than ground feeding, which may be the reason for the significantly higher T_b mean for the former in *Cyclura*. It may be especially important for large iguanas to be well heated. Taylor *et al.* (1972) calculated that a mouse could run vertically with a much smaller increase in oxygen consumption over level running (23.5 percent increase) than could a chimpanzee (189 percent increase) or a horse (630 percent increase). Fourthly, both digestive efficiency (Harlow *et al.* 1976) and peristalsis (Mackay 1968) are greater in the preferred T_b range, at least in *Dipsosaurus dorsalis* and *Ctenosaura pectinata*, respectively.

Cyclura did feed at T_b's below the regulating phase range. The amount consumed during this anticipatory feeding was usually less than at higher T_b's. It was clearly adaptive for a lizard to sample food near its burrow before or during morning basking or extended overcast while on a foray, before other foraging lizards found the source. Had a deterioration of the weather prevented the lizard from reaching or regaining the preferred T_b range after anticipatory feeding, the likelihood of an alimentary blockage was minimal since lizards could defecate at T_b's below the lowest field T_b recorded for ground feeding. As expected, *Cyclura* did not feed at T_b's below the lowest T_b recorded for emerging

lizards in the field. The same was true for *Anolis tropidolepis* (Fitch 1972) and *Sceloporus cyanogenys* (Greenberg 1976). Feeding T_b can be depressed in at least one captive lizard; *Amphibolurus fordi* fed at 12 C below minimum field T_b after several weeks in the laboratory (Cogger 1974).

The T_b at the initiation of foraging was depressed significantly during cooler weather. This may have been due to greater hunger during this time, rather than to lower environmental temperatures. Hunger depressed the T_b for emergence and the start of activity in *Cnemidophorus sexlineatus* (Hardy 1962). Although *Cyclura* fed all year, it shifted from a diet of flowers and fruits during warmer weather to leaves in cool, dry months like February (Auffenberg, in prep.). Guts were no less full than at other times of the year. However, passage times were not determined. Also digestive efficiency for leaves may have been lower than for flowers and fruits.

Comparative Thermoregulatory Behavior of Heliothermic Lizards

Taxonomic classification of lacertids based on differences in thermally related behavior agrees fairly well with classification based on morphology. For example, of 25 species of gekkonids examined, only two were diurnal and two diurno-nocturnal; the rest were strictly nocturnal (Werner 1969). Obviously, nocturnal activity adds another dimension to thermally related behavior not found in families of strictly diurnal lizards. Secondly, a few lizard families (Anelytropsidae, Anniellidae, Dibamidae, Feylinidae, and Pygopodidae) consist primarily of fossorial members, which must thermoregulate thigmothermically, if at all. The majority of lizards show at least some degree of

heliothermality (Porter 1972). Thirdly, members of the Lacertidae, Scincidae, Teiidae, and Varanidae are unable to change their integumental coloration, whereas most agamids, chamaeleonids and iguanids can (Norris 1967). Fourthly, panting, gular flutter, gular pumping, and gaping behaviors appear to be restricted to specific families or groups of families (Heatwole *et al.* 1973). Agamids, iguanids, and gekkonids pant; that is, they open their mouths at high T_b's and increase their respiratory rate, resulting in head cooling by evaporation of water. Only gekkonids engage in high frequency gular flutter just prior to panting. Varanids don't pant. Instead, they engage in a high amplitude, low frequency gular pumping (Johnson 1972). Panting is also poorly developed or absent in the skinks. *Egernia hosmeri* gapes, opening its mouth without increasing respiratory or heart rate (Webb *et al.* 1972). *Tiliqua rugosa* and *T. scincoides* "gulp," opening their mouths only during inhalation (Heatwole *et al.* 1973). *Eumeces obsoletus* and *Mabuya striata* do not open their mouths at all at high T_b's (Richards 1970).

It would be unwise to define species and genus level phylogenetic homologies based on thermally related behavior. Normally, as the similarity of an innate behavioral pattern in a group of species increases, the probability of common origin also increases. However, since the laws of heat transfer are constants, similar thermally related behaviors can just as easily evolve independently in distantly related species, when they are of similar size and shape and occupy similar habitat types.

Many differences between thermally related behaviors in lizard species are due to differences in adult body size. Firstly, large size intrinsically limits what the lizard can do. *Dipsosaurus dorsalis* elevated its T_b an average of 7.9 C while in its burrow prior to morning

emergence (McGinnis and Dickson 1967). The time of emergence of *Podarcis muralis* correlated directly with the timing of sun warming of the lizard's retreat (Avery 1978). These two iguanids may or may not bask covertly in the same manner as the gekkonid *Coleonyx brevis*, which assumes an elevated posture in its rock shelter and makes contact with the sun-heated roof (Dial 1978). Larger lizards such as *Cyclura carinata* were not found to bask covertly in sand burrows, probably due to the thickness of the burrow roof near the mouth and to the common placement of the burrow mouth under vegetative cover. It would be a mistake to assume that larger lizards never bask covertly, however. *Sauromalus obesus* didn't emerge until the late afternoon during hot days on the Mojave desert. Individuals had reached T_b's of 43 to 46 C inside their rock crevice retreats and were emerging to cool rather than to bask (Case 1976)! Secondly, lizards which spend part of their lives buried in direct contact with sand; for example, members of the genera *Uma* and *Phrynosoma*, are all small. Obviously, large lizards would find it more difficult to bury themselves. Instead, they retreat to predug burrows, natural rock crevices, or hollow trees. Thirdly, arboreality is more common among small lizard species. Not only is climbing relatively more energetically expensive than level walking as body weight increases (Taylor *et al.* 1972), but also the variety of vegetation capable of supporting the lizard's weight decreases. Although *Cyclura carinata* is clearly a capable bush and tree climber, the larger *Cyclura stejnegeri* (Wiewandt 1977) and *Conolophus subcristatus* (Werner, D., personal communication) rarely climb in vegetation as adults. Juvenile *C. stejnegeri* are frequent climbers. The large *Cyclura pinguis* is only an "occasional" climber in low bushes (Carey 1975).

As the adult body weight of a lizard species increases, the surface to volume ratio decreases. This change imposes at least three changes in the heating and cooling characteristics of the lizard's body, which in turn alters the thermoregulatory behavior.

Firstly, the rates of heating and cooling decrease and the thermal lag time increases as body weight increases. For example, an *Uta stansburiana* hatchling (0.3 g) in its dark phase heated at a rate of 13.2 C/min in direct midday sun, while a 50.8 g *Dipsosaurus dorsalis* in its dark phase heated 7.3 times more slowly (Norris 1967) and a 645 g *Cyclura carinata* heated maximally 37.6 times more slowly. The expected longer morning basking time in larger lizards doesn't necessarily occur, however. Adult *Iguana iguana* omitted the morning basking period in August, exposing only parts of their bodies to the sun and then only for short durations (McGinnis and Brown 1966). Thermal comfort postures are defined as those associated with high T_b and probably function to relieve thermal stress on all or part of the lizard's body (Greenberg 1976). Elevation of the tail, toes, legs, and trunk off of hot substrates as well as panting and retreat to the shade are included. These behaviors appear to be more commonly observed in small lizards, again probably due to their higher heating rates. For example, *Sceloporus cyanogenys* may lift all four legs and rest with only its ventrum on the hot substrate (Greenberg 1977). *Cyclura carinata*, on the other hand, may briefly elevate its digits off of hot substrates, but usually walks into the shade instead. Four of five species of *Cnemidophorus* studied by Schall (1977) consistently raised their digits during basking. *Cyclura carinata* did not. Panting is an infrequent behavior in heliotherms in general, but is probably more infrequent in large lizards. It usually occurs only

when the animal is forced to stay in the open; for example, during day long, male-male fights in *Conolophus cristatus* (Werner, D., personal communication), nesting in female *Cyclura stejnegeri* (Wiewandt 1977), and scaring into the open by man in *Iguana iguana* (McGinnis and Brown 1966). The length of the daily activity period may increase with body weight. When the frequency distributions of the time of collection of thirteen *Ctenotus* species (Pianka 1969) were arranged according to increasing snout-vent length, the midday active species were small, the bimodally active species were larger, and the all day active species were largest. Lastly, the increasing thermal lag time as body weight increases may result in a larger midday depression of the T_b's for seeking shade and sun. This hypothesis has not been tested as yet.

Secondly, the effectiveness of forced convective heating and cooling decreases as body size increases (Muth 1977b, Parry 1951, Porter and Gates 1969, Spotila *et al.* 1972). During early morning basking several small lizards have been reported to assume an elevated posture (Greenberg 1977, Hardy 1962, Heatwole 1970, Muth 1977b). Not only does this posture reduce heat loss to cool substrates, it also increases convective heating by warmer air further off the ground. No large lizard has been reported to bask in the morning in a completely elevated posture. Muth (1977a) recognized three thermoregulatory postures in *Callisaurus draconoides*; prostrate, tail down, and elevated. In field caught lizards these postures corresponded to mean T_b's of 33.9, 40.5, and 42.7 C, respectively. A maximally elevated posture is especially effective in convectively cooling a small lizard, exposing the trunk to higher wind velocity and lower air temperature. Convective heat loss more than balances the increased radiant heat gain in this posture (Muth 1977b). Again, the

maximally elevated posture is uncommonly seen in large immobile lizards with high T_b's. Arboreal behavior should also be more effective as a morning heating technique (Bradshaw and Main 1967, Cogger 1974, Heatwole 1970) and midday cooling technique (Axtel 1960, Bradshaw and Main 1967, Judd 1975, Norris 1953) in small lizards. Since arboreality is better correlated with high surface temperatures in small lizards, the behavior is more clearly restricted to narrow time bands during the summer day. Lastly, high winds should be more frequently a cause of premature submergence in small lizards (Bradshaw and Main 1967, Bostic 1966, Mayhew 1963).

Thirdly and lastly, large lizards are more tightly coupled to the solar and thermal radiant environment than small lizards (Norris 1967, Porter and Gates 1969, Spotila *et al.* 1972). Large lizards can sustain a larger change in air temperature and a smaller change in absorbed radiation while maintaining a constant body temperature. Thus, large lizards reach higher equilibrium temperatures in the sun (Parry 1951, Porter and Gates 1969), partially explaining why most of the reptiles with high late afternoon maximum T_b's are large. Of course, the greater late afternoon, high T_b tolerance than earlier in the day contributes to the response. The stronger radiant coupling in large lizards also results in a more sustained utilization of sun orientation throughout the day; that is, less random orientation during the activity period than in small lizards. Another result of high radiant coupling and low convective coupling may be Norris's finding (1967) that large lizards, defined as having a surface to mass ratio greater than 3.5 and a body weight greater than 40 g, are more reflective in both the ultraviolet and infrared radiation ranges than small lizards.

The environmental temperatures faced by a lizard, controlled by habitat variations in vegetational cover, elevation, and latitude, have a considerable influence over interspecies differences in thermoregulatory behavior. The number of times a lizard basks in the sun each hour, called the basking frequency, as well as the mean length of basking and shade sitting time periods, show distinct species specific differences correlated with the openness of the species' habitat (Spellerberg 1972d). *Sphenomorphus quoyi* had a high shuttling frequency and low mean basking and non-basking intervals. The species lives in open rocky areas on river banks, where exposed areas become quite hot and rocky crevice retreats remain quite cool. A high basking frequency permitted maintainance of a stable regulating phase T_b in a habitat where high heating and cooling rates could not be avoided. *Sphenomorphus tympanum* (warm temperature) had about the same mean field T_b, yet had a longer mean non-basking interval, since shade temperatures in its open forest habitat were fairly high.

Integumental emissivity may vary in a consistent way with the ease of heating possible in a lizard's habitat. A low long wave emissivity could lead to overheating in a hot environment. Thus, a 0.965 value for *Sceloporus occidentalis* may be adaptive (Bartlett and Gates 1967). The 0.69 value for *Liolaemus multiformis* may also be adaptive, since it permits greater heat retention in a cold environment, the mountains of Peru (Pearson 1977).

The tropics are characterized by greater thermal and photoperiod constancy than temperate regions. One would expect this to result in some basic differences in the thermal biology of animals living in the two areas. For example, acclimation ability should not be selectively

advantageous in the tropics. The CTMax of temperate zone fiddler crabs could be markedly reduced by lowering the acclimation temperature, whereas tropical forms did not respond (Vernberg and Tashian 1959). Two temperate zone salamanders had decreasing standard rates of metabolism with increasing acclimation temperature while two tropical zone species were unaffected (Feder 1978). Feder (1976) also found that tropical salamanders consumed less oxygen while at rest than temperate zone species of similar body weight. In contrast to fiddler crabs, tropical amphibians did not maintain unaltered CTMax's when acclimation temperature was changed. Although the CTM increased as the species latitude of distribution decreased, acclimation ability did not decrease (Brattstrom 1968). Comparative studies of acclimation ability in temperate vs. tropical lizards are rare. However, Clark and Knoll (1974) found a direct correlation between mean T_b and latitude in 28 *Anolis* species. The majority of the correlation could be accounted for, through multiple regression, by the lower light level in the tropical habitats. However, a significant portion of the correlation was dependent on latitude alone. The authors hypothesized that raising the MBT at higher latitudes was adaptive, permitting growth, reproduction, and other activities to proceed at faster rates in the shorter time frame.

What are some of the interspecies differences in thermoregulatory behavior of heliothermic lizards which cannot be explained by differing body sizes, environmental temperatures, and habitats? First, lizards orient to the sun in two different ways during morning basking. One group, consisting of several *Amphibolurus* species (Bradshaw and Main 1967, Cogger 1974, Heatwole 1970), *Holbrookia propinqua* (Judd 1975), and *Sceloporus cyanogenys* (Greenberg 1976), bask in a positive parallel

orientation. The other group, including *Amphibolurus barbatus* (Lee and Badham 1963), *Conolophus subcristatus* (Werner, D., personal communication), *Cyclura carinata*, and *C. stejnegeri* (Wiewandt 1977), *Leiolopisma fuscum* and *L. rhomboidalis* (Wilhoft 1961), and several species of *Phrynosoma* (Heath 1965), bask positive normal as well as positive parallel. The seasonal orientation shifts in *Cyclura carinata* and *Phrynosoma* are approximately the reverse of one another; that is, *Cyclura* basks positive parallel more frequently during low winter temperatures whereas *Phrynosoma* only basks positive parallel above air and substrate temperatures of 20 C. *Amphibolurus barbatus* orients positive normal on the ground and positive parallel on logs. When observed over a wide range of environmental temperatures and under varied habitat topographies, other heliothermic lizards may also demonstrate this orientation flexibility. Presumably, the orientation assumed usually results in maximization of the heating rate.

Secondly, most heliothermic lizards, if they rest on the ground at all, are variably prostrate during morning heating (Bartholomew 1966, Bostic 1966, Bradshaw and Main 1967, Carey 1975, Cogger 1964, Hardy 1962, Lee and Badham 1963, Judd 1975, Muth 1977a, Norris 1953, Werner, personal communication, Wiewandt 1977). Knowing that the degree of substrate contact varies with disturbance due to the observer, substrate temperature, and wind velocity, and without interspecies comparisons under identical field conditions, it is unwise to hypothesize a genetic basis for the minor species differences evident from a search of the above literature.

Thirdly, several thermal comfort postures are not universally present in heliothermic lizards. Toe reflexion occurs in at least seven

species of *Cnemidophorus* (Bostic 1966, Kennedy 1968, Schall 1977). It is present in *Cyclura carinata*, *Dipsosaurus dorsalis* (Norris 1953), and *Sceloporus cyanogenys* (Greenberg 1976), but is absent in *Amphibolurus inermis* (Heatwole 1970). Shovelling behavior occurs in at least *Dipsosaurus dorsalis* (Norris 1953) and *Uma* sp. (Stebbins 1943) and very rarely in *Cyclura carinata*, but is absent from all *Amphibolurus* species studied by Bradshaw and Main (1967).

Complexity of Social Behavior in *Cyclura carinata* as a Function of Latitude

Avery (1976) believes that the complexity of diurnal lizard social behavior or, at least, the potential for increased social complexity, increases as the species' latitude of distribution decreases. *Lacerta vivipara* ranges further north than any other lizard, yet retains a preferred T_b nearly as great as its southern relatives. Thus, the activity period is shorter, requiring an increased percentage of active time devoted to thermoregulation and foraging at the expense of social interaction. This may have mandated the evolution of its simple social system, characterized by a lack of territoriality and little interaction between individuals. As hypothesized, lacertid territorial systems and territorial and courtship display signals are more elaborate in more southerly lizard species.

Cyclura carinata's social behavior is moderately complex, as expected by Avery's hypothesis. Dominant males are territorial year round, and territories are fairly rigid, at least where food is abundant. Local males form a dominance hierarchy based primarily on body size. Females, however, are only territorial during the nesting season. Specific male-male and male-female interactions are long term in this long-lived

lizard. Yet, the social repertoire appears no more complex than in other tropical iguanids. *Cyclura carinata* spends an average of 26.5 percent of the total yearly time above ground. This fits in nicely between the values for *Podarcis muralis* (19 percent at 44° N) and *Agama agama* (31 percent at 11° N)(Avery 1976, Figure 6, p. 254). *Cyclura*'s social system, more complex than *Podarcis*'s and less complex than *Agama*'s agrees with expectation.

Nocturnal Lizard Aggregations

The cooling rate of a reptile decreases as intrasurface contact increases and intersurface contact with cooler air and substrate decreases. For example, the carpet snake, *Morelia spilotes*, reduces heat loss gained during basking by tightly coiling its body (Cogger and Holmes 1960) and brooding *Python molurus bivittatus* reduces metabolically produced heat loss by coiling around its eggs (Hutchison *et al.* 1966, Van Mierop and Barnard 1976). Survival of snakes in temperate region hibernacula is probably enhanced by the thermal protection of the site, rather than by any thermal benefit derived from direct contact of individuals (Aleksiuk 1976). This does not always appear to be true in the tropics; for example, *Boa constrictor* daily basks outside its hibernaculum (Myres and Eels 1968). *Sauromalus varius* and *S. hispidus* aggregate in single species, mixed sex groups of up to seven individuals (Case 1978). Digestive efficiency during the initial nighttime hours must be greater in these groups than in lizards which retreat singly into burrows and rock crevices. *Amphyrhynchus cristatus*, living on exposed lava flows in the Galapagos, forms what must be purely thermoregulatory nocturnal aggregations, consisting of piles of up to 50 individuals, eight animals

in depth (White 1973). The large size of these unique aggregations is undoubtedly related to the high localized diurnal density in this species coupled with the small size of the breeding territories. Nighttime aggregations of more than two *Cyclura carinata* were not observed in the field. The group always consisted of a male and a female. The same pattern has been reported for *Sauromalus obesus*, another highly territorial iguanine (Case 1978). Long term burrow pairings in *Cyclura carinata*, lasting at least 17 days, were only observed during my February trip, but may extend into May. Male interest in females during the day increased in late March through April, culminating in mating in late April and May (Iverson 1979). Thus, temporary burrow sharing may serve a reproductive function, such as enhancement of egg development or female receptivity, rather than a thermoregulatory function. Burrow sharing may have been more frequent in areas where preferred retreats were more limited and sufficient food was available to support a high lizard density. All seven adults in the Gainesville pen squeezed into a short burrow recently dug by an adult female, rather than using the previously occupied plywood boxes. Short term pairings, as when two individuals retreated into the nearest burrow at the start of a heavy rain or upon my approach, were observed in all seasons.

Physiological Considerations

Aerobic vs. Anaerobic Metabolism

In many lizards more energy is derived anaerobically than aerobically during maximum exercise. Between 60 and 80 percent of the energy utilized during a 2 minute activity period by *Dipsosaurus*

dorsalis between T_b's of 25 and 45 C was anaerobically produced (Bennett and Dawson 1972). This range is conservative since some aerobiosis is applied to the oxygen debt. Similar results were obtained for *Sceloporus occidentalis* (Bennett and Gleeson 1976). Whole body lactate was not determined for *Cyclura* during exercise and, thus, an estimate of anaerobic energy production could not be made. Nonetheless, the large recovery oxygen volume does indicate a heavy reliance on anaerobiosis. Assuming that the rate of oxygen consumption measured immediately at the end of the exercise period was a good estimate of the consumption rate during exercise, recovery oxygen was equal to 70, 71, 71, 73, 76, and 81 percent (T_b = 15, 20, 25, 31, 37, and 42 C, respectively) of the total oxygen consumption above the resting level during and after exercise.

The anaerobic contribution to energy production in lizards varies with the length of the exercise period (Bennett and Licht 1972). More than 50 percent of the total lactate produced during exercise to exhaustion occurred during the first 30 seconds in several species. This initial maximum lactate production rate corresponded to the highest activity rate. An initial burst of activity is typical of iguanids and probably corresponds to high speed territorial chases and escapes in free-ranging animals.

The aerobic contribution to activity should be greatest in the preferred T_b range, where oxygen scope is often greatest (Bennett and Dawson 1976, Dawson 1975). For example, anaerobic energy production was approximately 60 percent of the total at 20 C, but only 36 percent at 37 C over 5 minutes of activity in *Uta stansburiana* and *Cnemidophorus tigris* (Bennett and Licht 1972). The tapering off of maximum oxygen consumption at high T_b in *Cyclura* was probably due more to a maximization

of oxygen affinity and capacity of the blood due to high temperature than to an increasing effect of decreasing pH on oxygen transport, due to an increasing blood lactate level (Bennett 1973). Both resting and maximum activity levels of whole body lactate were essentially independent of T_b over a wide range in all lizards examined except in *Dipsosaurus* (Bennett and Licht 1972) and *Sceloporus occidentalis* (Bennett and Gleeson 1976), with peak maximum production at T_b's of 40 and 30 C, respectively.

Clear evidence of a high correlation between exhaustibility and life style has been found for a number of amphibians and reptiles. *Scaphiopus hammondii* and *Bufo cognatus* both failed to fatigue after long exercise periods, whereas *Rana pipiens* and *Rana catesbiana* fatigued rapidly (Seymour 1973). The maximum oxygen scopes for these anurans were, respectively, 1.22, 1.36, 0.32, and 0.16 $cm^3/(g \cdot hr)$. The latter two species rely on a quick jump to water to escape predation. The high scopes of the former two may be related to their greater digging proclivities. Bennett and Licht (1974) found similar results for *Rana pipiens* and *Bufo boreas*. The former had a high anaerobic capacity which it used for rapid flight from predators. The latter had a low anaerobic capacity and did not exhaust during its slow movements, relying on noxious skin secretions and bloating to foil predators. *Thamnophis sirtalis* adults took as long as 20 to 27 minutes to reach exhaustion, presumably because they must subdue slowly exhausting mammalian prey (Pough 1977). *Coluber constrictor* and *Masticophis flagellum* both were still active after 5 minutes of exercise, whereas *Crotalus viridis* was completely exhausted. *Lichanura roseofusca* intermittently coiled into a defensive ball after only 1-2 minutes (Ruben 1976). These differences were clearly reflected in both higher aerobic and higher

anaerobic capacities for the more active snakes. *Varanus gouldii* was found to be much less susceptible to fatigue than *Sauromalus hispidus* (Bennett 1972). The former escaped exhaustion through a combination of better blood buffering, more efficient lung structure, and higher levels of muscle myoglobin than the latter (Bennett 1973).

All behavioral motions of *Cyclura* were of relatively short duration, alternating with periods of quiescence. In the Gainesville pen 77.1 percent of lizard movements during the time-motion study lasted less than 6 seconds. Motions lasting 30 to 60 seconds constituted only 0.7 percent of the total.

Walking, the most commonly observed behavior, was probably a primarily aerobic activity. Aggressive tracking of habituated adults, by repeated approaches to distances resulting in lizard withdrawals, could be continued practically indefinitely. Lizards usually moved only a few meters before stopping. *Amblyrhynchus cristatus* adults swam at an average speed of 27.2 m/min, the "cruise velocity," without greatly raising blood lactate level (Bartholomew *et al.* 1976). Lizards swimming at "burst velocity" averaging 44.6 m/min or 1.64 times as fast, did exhaust. These two swimming speeds are probably analogous to walking and fast running speeds in *Cyclura*.

More strenuous forms of behavior in *Cyclura carinata* were either of short duration and usually not immediately repeated (chases) or discontinuous, with pauses (climbing, digging, and fighting). Territorial chases never lasted more than a few seconds. Iverson (1979) found that only 7.5 percent of male-male encounters resulted in fights and these were also of short duration (N = 4, 30-70 sec). Sand kicking from burrows was a decidedly intermittent behavior, similar to that described

for *Scaphiopus hammondii* (Seymour 1973). These behaviors may well have resulted in substantial rises in lactate production. Yet, since *Cyclura* was fully capable of escape behavior just after completing any of these more strenuous activities, some anaerobic capacity must always be held in reserve. Any build-up of lactate could be at least partially removed during the pauses, especially if the iguana had reached preferred T_b. Bennett and Dawson (1972) and Bartholomew *et al.* (1976) have suggested that lizards are aware of their reserve capacity, through neural sensory inputs involving blood pH, $[H^+]/[OH^-]$ or P_{O_2} and reduce activity to an aerobically sustainable level long before an incapacitating debt is incurred. Nonetheless, a daily buildup of lactate may result in decreased or abbreviated activity. Protracted copulations, fighting, chases, and nesting in field cages or the Gainesville pen did result in decreased activity for the rest of the day. The lowest daily lactate concentration probably occurred just before morning preemergence burrow movement. The timing of maximum activity in midmorning to midday may in part be due to this low lactate level. Liver removal of high blood lactate levels commonly takes a long time in reptiles. Blood and liver lactate in *Natrix rhombifera* required 7 hours to return to resting levels after only 10 minutes of maximum activity at 35 C (Gratz and Hutchison 1977). Five hours after a 1 hour dive, *Chelonia mydas* had removed only one-half the lactate produced (Berkson 1966).

Why do lizards commonly rely on anaerobic energy production, when the incapacitation resulting from a high lactate level obviously increases the animal's vulnerability? Bennett and Licht (1972) argue on energetic grounds. Lizards operate over a wide range of body temperatures. To provide a rapid responsiveness aerobically over the full T_b range would

require a high basal rate of metabolism. Anaerobic readiness, on the other hand, does not require a high resting metabolic rate, yet is available at all times. Its effectiveness is also essentially temperature independent.

Cyclura carinata fled from predators rather than relying on a static defense, as do some amphibians and reptiles with lower rates of maximum oxygen consumption (Bennett and Licht 1974, Ruben 1976). The animal was familiar with the location of burrows outside its usual home range, to which it could escape when caught far from one of its home burrows (Iverson 1977). Thus, the location of infrequently visited burrows must be remembered for long periods. Nonetheless, dogs and cats, introduced onto Pine and Water Cays during the present study, ran down adult iguanas before they reached their burrows. When halted short of a burrow, partially exhausted iguanas may have resorted to a defensive bloat or a prostrate posture, as observed in the laboratory. Reliance on a quick escape provided primarily by anaerobiosis clearly proved ineffective against large carnivores since the *Cyclura* population plummeted to zero within 2 years after the cat and dog introduction (Iverson 1979). Direct killing and habitat destruction by man were also important contributions to the population decline.

Neural Basis for Shuttling Behavior in Lizards

The problem of locating the neurons which control lizard thermoregulatory behavior has been approached in two ways; that is, either by monitoring various characteristics of neuronal action potentials during heating and cooling of preparations or by monitoring thermoregulatory behavior in intact animals during or after various manipulations. Taking

the first approach, Cabanac *et al.* (1967) recorded the firing rates of neurons in the putative thermoregulatory brain center while heating and cooling the area with a thermode. Also, recordings of peripheral nerve modalities during local heating and cooling have indicated the presence of thermal receptors in the integument: Iggo (two mammals, 1969), Bailey (lizard, 1969), Kenton *et al.* (caiman and alligator, 1971), Necker (caiman, 1974), and Spray (frog, 1974). The simplest approach in the intact animal studies is to implant one or more thermocouples or thermistors and observe either shuttling behavior in a thermal gradient (Berk and Heath 1975a, Barber and Crawford 1977 and 1979) or thermal operant behavior (Garrick 1979). Technically more sophisticated approaches involve implanting a thermosensitive region of the brain with a thermode (Hammel *et al.* 1967, Myhre and Hammel 1969) or producing a localized brain lesion (Kluger *et al.* 1973, Berk and Heath 1975b). Biochemical approaches have also proven fruitful. Lizards have been injected with pyrogens (see Kluger 1979 for a review) and putative transmitter substances (Bligh *et al.* 1976).

Hammel *et al.* (1967) and Cabanac *et al.* (1967) were the first to show that the preoptic area of the hypothalamus was involved in the control of thermoregulation in lizards. Berk and Heath (1975b) subsequently found evidence for involvement of the medial and periventricular preoptic areas, nucleus of the anterior hypothalamus, nucleus suprachiasmaticus, paraventricular nucleus, medial wall of the telencephalon, and the ventro-medial telencephalon. The posterior hypothalamus (Kluger *et al.* 1973-lizard), the medulla (Lipton 1971-rat), and the spinal cord (Rautenberg 1969-pigeon, Thauer 1970-rat) may also have controlling influences on thermoregulatory behavior in lizards. The

parietal eye-pineal organ-parapineal organ complex also influences thermoregulatory behavior in lizards (Ralph *et al.* 1979). Peripheral thermal receptors in the integument clearly have an effect (Myhre and Hammel 1969, Cabanac and Hammel 1971, Barber and Crawford 1979, present study). Despite all of this work, however, the identification of neural control tissues and the pathways between them and the effector tissues remains far from complete.

Lizard thermoregulatory control has been called "broad band" (Bligh 1966), "coupled on-off" (Heath 1970), "stochastic dual-limit" (Barber and Crawford 1977), and "duel threshold" (Barber and Crawford 1979). Lizards have coarse T_b control, which they maintain primarily behaviorally. However, mammalian fine control mechanisms; that is, nonshivering thermogenesis, piloerection, shivering, insensible perspiration, and sweating, are lacking in lizards. Only vasomotor control has been demonstrated. Lizards have two distinct T_b "setpoints" (Heath 1970), a maximum and a minimum, and a refractory range in between where shuttling behavior, but not proportional control, is in abeyance. For example, in a two temperature, forced convection chamber that was heated or cooled depending on which end of shuttle board *Dipsosaurus* was sitting on, shuttling ceased when the cold temperature was elevated to 36 C or the hot temperature was lowered to 43 C, leaving a refractory zone of approximately 7 C (Barber and Crawford 1979).

The neural basis of lizard thermoregulation was considerably clarified by Cabanac *et al.* (1967), who discovered two groups of temperature sensitive neurons in the hypothalamus of the skink, *Tiliqua scincoides*. One group, called cold-sensitive neurons, increased their firing rate with decreasing brain temperature. Another group, the

warm-sensitive neurons, increased their firing rate with increasing brain temperature. Most of the neurons recorded fell into a third group, the temperature insensitive neurons, which did not change their firing rate with increasing brain temperature. Similar firing rate patterns have been found in the recordings of mammalian hypothalamic neurons (see Bligh and Moore 1972 for a review). The problems with Cabanac's study were the small number of neuronal recordings, the failure to record the change in firing rate over the full temperature range of each neuron, and the failure to consider other neuronal modalities, such as spike amplitude. Also, for some reason, no one has followed up on the study using other reptiles.

Hammel (1965), thinking of mammals, was the first to hypothesize how warm and cold neurons interact to determine the T_b setpoints. Heat producing mechanisms (or shuttling into sunlit areas in the case of lizards) may be initiated when the firing rates of the cold-sensitive neurons exceed the rates of the temperature insensitive neurons, which act as inhibitory references. Heat dissipating mechanisms (or shuttling into the shade in lizards) may be initiated when the firing rate of the warm-sensitive neurons exceed those of the insensitive neurons. Since many neurons in each of the three groups are probably involved, each with a different Q_{10} for firing rate or a different constant firing rate level, the setpoints probably result from an integrative averaging of many different firing rates.

Lizard setpoints are not fixed, but rather shift simultaneously either up or down in response to numerous stimuli: digestive state (Regal 1966-snake, Gatten 1974c-turtle), reproductive state (Garrick 1974), thyroid function (Wilhoft 1966), darkness (Regal 1967, Vernon and Heatwole

1970), inter- and intra-individual variation (present study), fever (Kluger 1979), and parietalectomy (Roth and Ralph 1976 and 1977). Three hypothalamic neuron changes have been proposed to account for these changes in setpoint, in accordance with the Hammel model. First, the constant firing rate of the temperature insensitive neurons could increase or decrease. An increase in firing rate above that of the cold neurons was proposed by Berk and Heath (1975a) as the mechanism for nightly voluntary hypothermia in diurnal lizards. However, since this would also result in the elevation of the upper setpoint, this is an unlikely explanation for the simultaneous depressions of upper and lower setpoints. Secondly, lines representing warm and cold neurons firing rates vs. ambient temperature could shift simultaneously and in the same direction along the X-axis without changing slope, that is, sensitivity. Lastly, the Q_{10}'s of the temperature sensitive neuron firing rates could change. This has already been demonstrated for rabbits (Cabanac *et al.* 1968) and cats (Eisenman 1969) during pyrogen induced fevers. In both these cases the slopes of the cold neurons increased and the slopes of the warm neurons decreased, raising the setpoints. Temperature insensitive neuron firing rates were generally not effected by pyrogen administration. Data gathered in the present and other studies point to involvement in lizards of both X-axis shifts and Q_{10} changes, as will be discussed below.

Thermal gradient studies have revealed that the standard deviation of the mean minimum T_b is significantly greater than the SD of the mean maximum T_b for individual lizards of at least two species (Berk and Heath 1975a-*Dipsosaurus dorsalis*, Garrick 1979-*Sceloporus cyanogenys*). Although not true for *Cyclura*, the trend is in the same direction and,

as shown by the heating and cooling experiments, the SD of mean intestinal temperature for heat seeking behaviors was significantly greater than for heat avoidance behaviors (Table 21). As hypothesized by Berk and Heath (1975a) and Barber and Crawford (1979), the neurological basis for this consistency in lizards may be the greater firing rate Q_{10} for warm neurons than cold neurons found by Cabanac *et al.* (1967) for *Tiliqua*. Mammalian hypothalamic neurons may (Wit and Wang 1968) or may not (Cabanac *et al.* 1968, Eisenman 1969) show this characteristic. Q_{10}'s for peripheral thermosensitive neurons in the cat, monkey, and rat do (Iggo 1970). A second modality which may partially account for the observed SD difference in lizards is the range of ambient temperatures over which the receptors fire. The range was wider for rat scrotal cold receptors than for warm receptors (Iggo 1969). Unfortunately, the reported lizard data to date are limited to recordings from only eight temperature sensitive hypothalamic neurons (Cabanac *et al.* 1967).

The larger Q_{10} for the firing rate of warm neurons than cold neurons may also be the cause of the negative skew for *Dipsosaurus* T_b frequency distributions, first reported by DeWitt (1967) and more recently found in a number of other poikilotherms by DeWitt and Friedman (1979) as well as the present study. Inter-species increases in field operant T_b's (Bogert 1949, Pianka 1969) are coupled to some extent with higher negative skew in their T_b frequency distributions. The same may be true for panting frequency distributions (Heath 1965). If an increase in mean T_b is the result of a simultaneous increase in the Q_{10} of the cold neuron firing rate and a decrease in the Q_{10} of the warm neuron firing rate, theoretically resulting in an increase in the negative skew of the T_b frequency distributions for both minimum and maximum

T_b's, then the overall T_b frequency distribution should also become more negatively skewed as mean T_b increases. Indeed, both the skews for minimum and maximum T_b in *Cyclura* summer lizards became more negative as their respective mean temperatures increased (Figure 74). As the firing rate slope for the cold neurons increased, the standard deviation of the mean minimum T_b should decrease, as was the case. However, the standard deviation of mean maximum T_b also decreased, though somewhat more irregularly, even though it would be expected to increase based on a decreasing Q_{10} for the warm neuron firing rate. Perhaps, peripheral input overrode the hypothalamic warm neuron influence at high T_b. On a lizard by lizard basis, there was no correlation between the standard deviations of the means and either mean minimum or mean maximum T_b. It may be unwise at this time to draw any conclusions concerning the relationship between temperature sensitive neuron firing rate Q_{10} and the variation in mean T_b.

For individual *Dipsosaurus* (Berk and Heath 1975a) and *Cyclura*, the SD of the mean for minimum T_b's was directly and linearly related to the SD of the mean for maximum T_b's. The distance up the SD_{max} vs. SD_{min} line in *Cyclura* was almost significantly, indirectly correlated with body weight (N = 12 field lizards, r = -0.414). Thus, increasing thermal lag with increasing body weight may be the explanation for this SD correlation, rather than having a neurological basis. The smaller linear correlation for SD_{max} vs. SD_{min} for the smaller *Dipsosaurus* also agrees with this explanation (r = 0.435 for *Dipsosaurus*, 0.804 for *Cyclura*, both in the thermal gradient). However, the correlation of distance out the line vs. body weight was not calculated for *Dipsosaurus*, since body weights of individual lizards were not reported (range = 27-60 g). The more

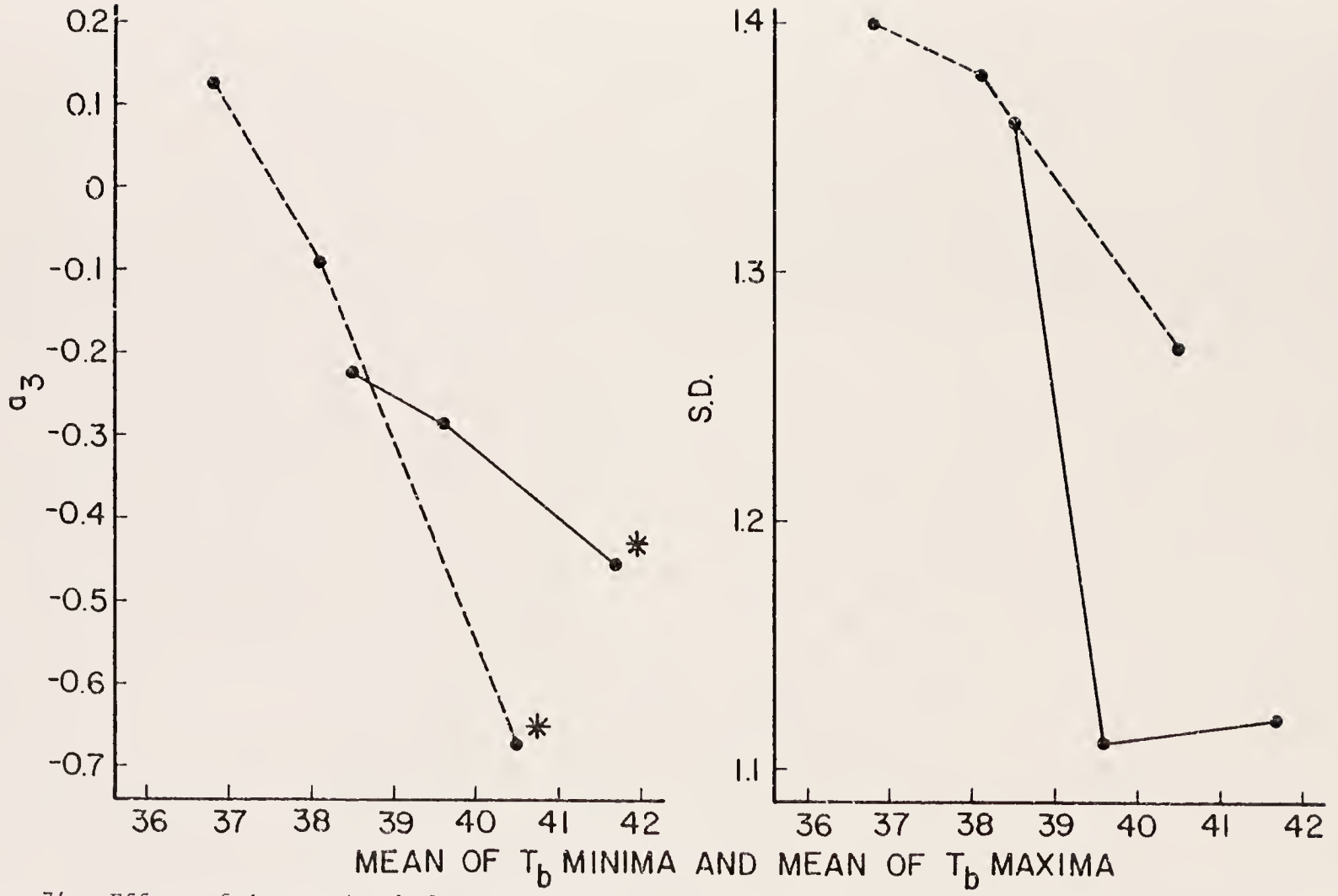


Figure 74. Effect of increasing body temperature on frequency distribution skew and standard deviation of the mean of T_b minima and T_b maxima. The three samples consisted of the highest, mid-range, and lowest mean T_b days of data (maximum of two days per lizard) for eight summer field lizards. All minimum and maximum T_b's for each day were used except those resulting from burrowing and cloud cover. Minimum T_b's are represented by dashed lines, maximum T_b's by solid lines. The asterisks indicate that the skew was significantly negative ($p \leq 0.05$ for maximums, $p \leq 0.01$ for minimums).

rapid increase of SD_{min} than SD_{max} in both *Cyclura* and *Dipsosaurus* is again suggestive of a higher Q_{10} for the warm neuron firing rate vs. ambient temperature.

Bligh (1972) has described a neuronal control model for mammalian thermoregulation which is applicable to lizards as well. The model consists of two main lines of central nervous system interneurons, one ultimately synapsing with motor neurons controlling shuttling into the shade and the other shuttling into the sun. Each line receives inputs from: 1) either stimulatory hypothalamic warm neurons (to the shade shuttling line) or cold neurons (to the sun shuttling line), 2) inhibitory hypothalamic temperature insensitive neurons, 3) non-thermal, inhibitory and stimulatory neurons from higher brain centers, 4) either stimulatory peripheral warm or cold receptor neurons, and 5) inhibitory neurons from the other line. One and two have already been discussed. Evidence for higher brain center inhibitory input in *Cyclura* is limited to the observation that shade seeking behavior can be temporarily overridden by feeding and social behaviors. Evidence for peripheral warm and cold receptors in lizards is mostly indirect. For example, high ambient air temperature in a shuttle box depressed the colonic temperature at exit (Myhre and Hammel 1969) and low T_a elevated it (Cabanac and Hammel 1971) in *Tiliqua scincoides*. Yet, peripheral input may be even more important than brain inputs in determining the shuttling setpoints, as indicated in the following three studies. First, direct heating of the preoptic region of *Tiliqua* decreased both the mean maximum skin temperature and maximum colonic temperature, while cooling increased the mean maximum and mean minimum skin temperatures and the colonic temperature (Myhre and Hammel 1969). Cooling the preoptic region approximately

10.7 C below control hypothalamic, shade-seeking temperature raised skin and colonic temperatures only 1.3 C, on the average (0.13 C increase per 1 C decrease in hypothalamic temperature). Heating the preoptic region 4.7 C decreased skin and colonic temperatures by 1.6 C, on the average (0.34 C decrease per 1 C decrease in hypothalamic temperature). Thus, considerable change in hypothalamic temperature was required to change skin and colonic temperatures. Also, skin and colonic maxima were three times more sensitive to an increase in hypothalamic temperature than a decrease. Secondly Bligh *et al.* (1976) found in *Varanus albigularis* that core temperature at the initiation of "panting" ranged from 35.4 to 38.6 C, while skin temperature varied hardly at all, indicating that the latter may be regulated. Thirdly, Barber and Crawford (1979) found for *Dipsosaurus* that while colonic temperature at exit from the hotbox decreased as air temperature increased, maximum skin temperature remained constant. They hypothesized that skin temperature rather than core temperature was being regulated.

Since mean minimum T_b increased faster than mean maximum T_b, the refractory interval in *Cyclura carinata* decreased as mean T_b increased, both within and between individuals (Figure 22 and Table 10). This was not just a result of seasonal differences in environmental temperatures, since summer data spanned the entire range in Figure 22, encompassing February and October results. Clearly, the relationship has adaptive significance. A lizard operating at high T_b is more likely to keep maximum T_b below a dangerous level than maintain a narrow range of minimum T_b's. Nonetheless, the two setpoints are coupled. The alternative, a narrowly variable maximum range uncorrelated with the minimum, would be disadvantageous for those individuals in the population

with the widest refractory range. In a large lizard like *Cyclura carinata*, too much time would be wasted seeking out and sitting in an appropriately cool spot before activity could begin again. When the Berk and Heath (1975a) and the Barber and Crawford (1979) data for *Dipsosaurus* were graphed in the same way as the field data for *Cyclura*, the correlations between mean high and mean low shuttling T_b's were not significant (linear correlation coefficients were 0.153 and 0.113, respectively). The mean maximum did not get above 43-45 C for a wide range of mean minimum colonic temperatures. This may have been due to the limitations of laboratory shuttle boxes, which are visually, thermally, and socially restrictive, as well as to the lizard's smaller size. Vaughn *et al.* (1974) did demonstrate that individual *Dipsosaurus* during fever have a shrinking refractory interval as mean T_b increased, with minimum T_b increasing faster than maximum. Also, mean maximum colonic and skin T_b were significantly correlated with mean minimum colonic and skin temperatures, respectively, in the larger *Tiliqua scincoides*, with mean minimum increasing faster than mean maximums (Myhre and Hammel 1969).

Garrick (1979) demonstrated a different pattern for a shrinking refractory interval in *Sceloporus cyanogenys*; that is, a more rapid decrease in mean colonic exit temperature than entrance temperature as heat lamp intensity increased. The *Sceloporus* response to high heat input was probably qualitatively identical to the midday depression in core T_b maxima and minima for *Cyclura* in the field. Higher peripheral input at maximum T_b due to higher peripheral temperature may be integrated with a lowered core input due to a greater surface-core temperature differential to produce a shade seeking shuttle at a lowered core temperature. The depression in minimum T_b after high intensity heating in

Cyclura and *Sceloporus* is harder to explain. In fact, Barber and Crawford (1979) reported no drop in minimum core or surface T_b with increasing hot chamber temperature in *Dipsosaurus*. The best explanation is that "shaded" air temperature in Barber andCrawford's shuttle box was kept constant, whereas it was definitely elevated under midday field conditions and also in the non-circulating air, operant conditioning apparatus used by Garrick. The resultant higher peripheral temperature during cooling would not only directly inhibit peripheral cold receptor firing, but, according to the Bligh model (1972), would also increase the inhibitory influence of any peripheral warm receptors.

The neurological basis for the narrowing of the refractory interval as mean T_b increased in *Cyclura* may be both a rightward unequal shifting along the X-axis of the firing rate lines for hypothalamic cold and warm neurons and an unequal change in the slope for the two lines (Figure 75). As mean T_b increased, the rightward shift in the cold neuron line may exceed that of the warm neuron line. This alone could account for the decreasing refractory interval. However, when the a_3's for the frequency distributions of minimum and maximum T_b's for the eight summer field lizards were plotted against mean minimum and mean maximum T_b, respectively, the lines were fairly linear, and the slope of the minimum T_b line was greater than the maximum (Figure 74). The skew of the distribution of minimum T_b's should become more negative as the cold neuron firing rate slope increases and the skew of the distribution of maximums should become more negative as the warm neuron firing rate slope decreases. These slope changes are also expected based on the firing rate responses of the hypothalamic warm and cold neurons in mammals during fever (Cabanac

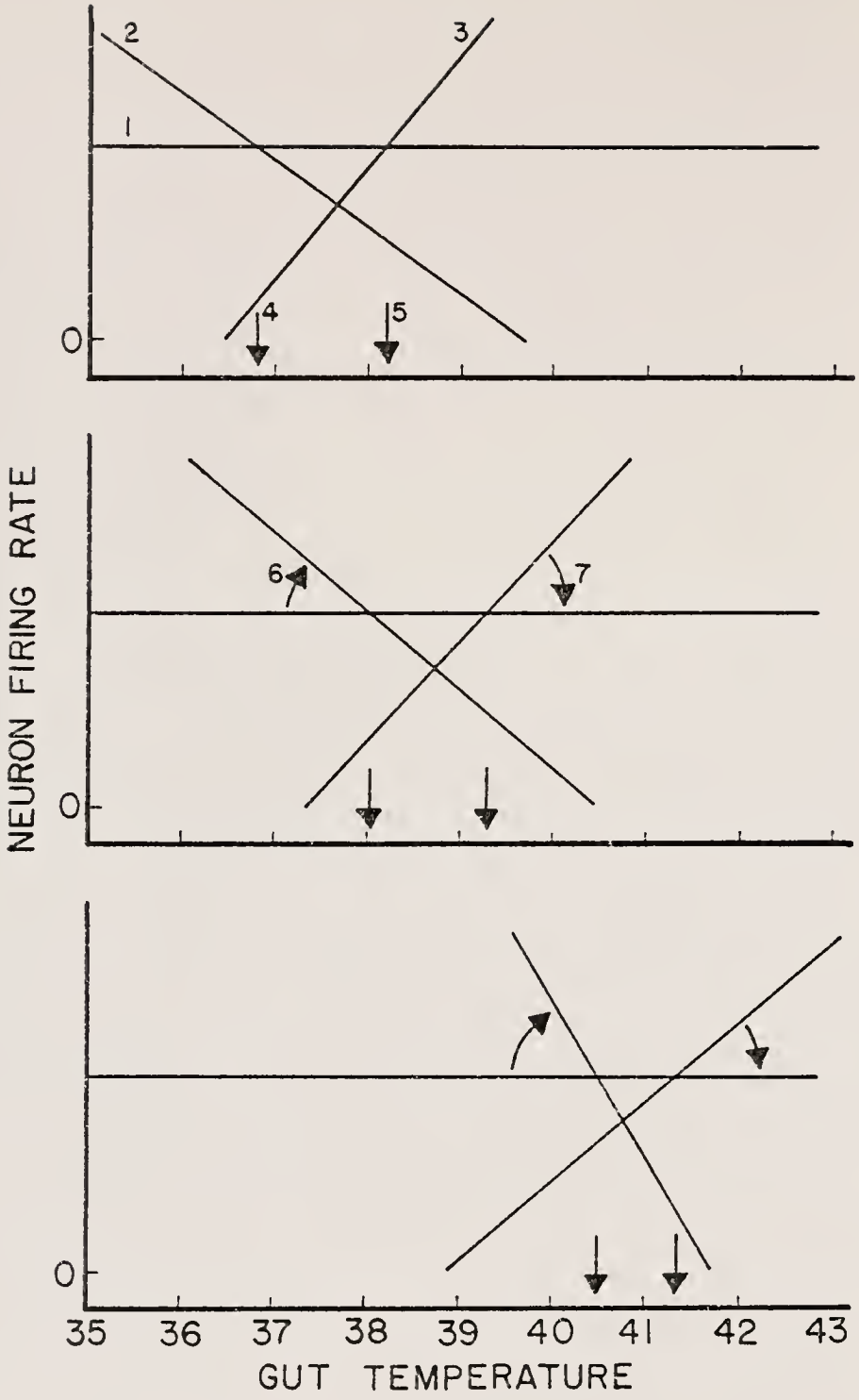


Figure 75. Hypothetical neural basis for changes observed during increasing mean body temperature in *Cyclura carinata*. Numbers 1), 2), and 3) indicate the firing rates of the temperature insensitive, cold, and warm neurons, respectively. Arrows indicate 4) the lower and 5) upper setpoints for T_b during the regulating phase and 6) the increasing and 7) decreasing firing rate slopes of the cold and warm neurons, respectively. The figure is modified from Berk and Heath (1975a).

et al. 1968, Eisenman 1969). If the slope changes occur in *Cyclura* as T_b increases, they would contribute to the decreasing refractory interval.

SUMMARY OF RESULTS AND CONCLUSIONS

1. *Cyclura carinata* is a diurnal heliotherm. Its T_b cycle can conveniently be divided into four phases: morning heating, regulating, evening burrow cooling, and nightly stable T_b. Mean field, regulating phase T_b ranged from 38.0 to 39.7 C, higher than for many other iguanids. Although faced with above lethal black body temperatures during part of the day over much of the year, iguanas were stenothermic during the regulating phase, with a mean range of only 3.3 C for all monitoring days.
2. Iguanas were initially hyperthermic in both the field and the thermal gradient. The mean time between release and the maximum hyperthermic response was 2.0 days in the field, with a mean maximum T_b range of 4.4 C. The hyperthermic responses may have been due to bacterial infection, transmitter meal, and thermal learning in coelomically implanted, transmitter force-fed, and thermal gradient individuals, respectively.
3. The 0.5 C seasonal variation in mean regulating phase T_b at Sitc II was close to the annual variation and expectedly low for a tropical lizard. Mean T_b did not correlated perfectly with seasonal variation in ambient temperatures; the October mean was 0.4 C higher than the warmer month of July. Summer mean T_b of nonhyperthermic iguanas was 1.6 C higher in sparsely vegetated Semi-open Scrub than in a mixture of Dense Scrub and Rocky Coppice. The difference was significant during hyperthermia as well. Mean T_b's were probably

even higher in Open Scrub, but iguana density was too low there to warrant monitoring. Iguanas thermoregulated as well in field cages with only burrow shade as in cages with burrow shade, vegetational shade, and elevated perches.

4. Mean preferred T_b did not differ significantly on any day of the first four days for iguanas acclimatized to summer vs. winter Gainesville temperatures, more extreme than in the Caicos. Thus, acclimatization to a temperature range as large as experienced in the field did not alter the acute (first day) nor final (fourth day) preferendum. However, winter means were significantly higher during the first two days than during the second two days in the gradient. The ranges of variation in both the field and gradient were less in winter, indicating a narrowing of temperature tolerance. Mean preferred T_b was lower than mean operant T_b in both summer and winter, the difference being greatest for the hottest environment, the least densely vegetated site in June.
5. Mean T_b probably did not differ with sex, with the exception of gravid females, which, based on one individual, had lower T_b's and weaker hyperthermic responses. On the average, adult females heated and cooled faster than adult males, simply due to their smaller size.
6. Mean regulating phase T_b decreased as overcast time increased, the correlation improving 2.8 times as environmental temperatures decreased from July to February. Continuous overcast had to be lengthy for T_b to fall below the mean minimum. T_b commonly increased initially during medium to heavy overcast, due to either or both thermal lag and iguanas seeking out hot substrates and assuming a prostrate posture when T_b was rising just prior to overcast and due only to the latter when T_b was falling just prior to overcast.

7. T_b was nearly independent of shaded air temperature, demonstrating the iguana's dependence on radiant heat gain. The mean $T_b - T_a$ difference ranged from 5.9 C in July to 11.0 C in February, with a minimum difference of 1.3 C and a maximum difference of 15.6 C. T_b was usually considerably less than sun exposed sand temperature, except early and late in the day and during extended overcast, when T_s decreased faster than T_b.

   Placing transmitter probes dorsal to the back, under the abdomen, and in the gut of iguanas in the Gainesville pen permitted a crude analysis of dorsal and ventral heat transfer, dividing the lizard's day between four heat transfer conditions. Iguanas were thigmothermic as well as heliothermic during part of the morning heating phase. During the morning portion of the regulating phase, they alternated between pure heliothermia (gaining heat dorsally, losing it ventrally) and losing heat both dorsally and ventrally. Pure thigmothermia (gaining heat ventrally, losing it dorsally) was rare, constituting only 2.5 percent of the active time. Thigmothermia, with or without dorsal heat gain, constituted only 20.7 percent of active time, nearly half during the short morning heating phase. Iguanas were heliothermic nearly 70 percent of the time. The number of heat transfer conditions was directly and linearly related to both mean T_b and to the total number of iguana movements.

8. Individual mean minimum T_b was highly correlated with mean maximum T_b, as was intraindividual change in minimum daily T_b vs. maximum daily T_b. The linear regression lines extrapolated to approximately the maximum voluntary tolerance, with the individual mean minimum T_b and intraindividual change in minimum daily T_b increasing faster than

the individual mean maximum T_b and intraindividual change in maximum daily T_b, respectively. Thus, the regulating phase T_b interval decreased as mean T_b increased. As a corollary, the SD of mean T_b also decreased as mean T_b increased.

A Berk and Heath (1975a) analysis of daily consecutive maximum-minimum and minimum-maximum T_b pairs in the field and the thermal gradient revealed a high positive correlation; that is, when the second maximum was greater or less than the first maximum, the second minimum was greater or less than the first, respectively. Daily and seasonal variation in this pattern correlated with daily and seasonal variation in ambient temperatures, at least partially explaining the high positive correlation.

The standard deviations of individual mean minimum T_b's were commonly slightly but not significantly greater than the SD's of maximum T_b's. Individual SD_{max}'s were directly and linearly correlated with their SD_{min}'s, that is, if an individual regulated its maximum T_b well, it also regulated its minimum T_b well. The correlation was in part a passive result of body weight variation, since the SD's increased non-significantly as body weight decreased. SD_{max} decreased faster than SD_{min}, expected since overheating was a more serious problem than a wide minimum T_b range.

Mean T_b was not correlated with body weight. Yet, large iguanas ($\bar{X}$ weight = 1446 g) were slightly but not significantly better thermoregulators than smaller ones ($\bar{X}$ weight = 729 g), no matter what their mean T_b. As mean T_b increased, mean SD decreased more rapidly in the larger individuals, which may be due to their greater danger of overheating due to thermal lag.

Overall frequency distributions of individual minimum and maximum T_b's were most commonly negatively and positively skewed, respectively, whereas individual T_b distributions of intermediate T_b's plus maximum and minimum T_b's tended toward negative skewness, both in the field and the thermal gradient. When individual T_b frequency distributions were examined on a daily basis vs. mean T_b, negative skew was most evident in the midrange of mean T_b's, and a weak, nonsignificant positive skew occurred at high mean T_b. The negative skew increased faster for the minima than for the maxima as their separate mean T_b's increased.

Results from minimum and maximum T_b analyses were interpreted in terms of the present limited knowledge of the neurological basis of lizard thermoregulation.

9. Maximum T_b most commonly occurred late in the summer day, especially among large males basking in the few remaining sunlit areas. This trend continued in February and, to a lesser extent, in October. Maximum daily T_b was also recorded during the final hour in the winter and summer thermal gradients, shifting to that time after four days in the gradient. It appears that *Cyclura*'s T_b tolerance is greatest at the end of the active period. In the field, heat exchange was usually in a brief equilibrium at this time since even though exposed substrates were hot, radiant flux was decreasing. Thus, if body surface temperature was regulated rather than the core, core T_b would tend to increase during this time. The gradient results point to a periodicity in temperature tolerance even in the absence of changing environmental temperature. A literature search revealed that most if not all lizards with higher afternoon T_b's are

large, which is expected based on their larger surface-core temperature difference and tighter coupling to radiant heat exchange at equilibrium.

Surface rather than core temperature may be regulated in *Cyclura*, as indicated by the above circumstantial evidence as well as four other points: 1. core temperatures were higher in October than July, 2. maximum, minimum, and panting threshold core T_b's all dropped to a minimum at midday, 3. the maximum T_b recorded during an overcast period was commonly higher than the preceding maximum, 4. during radiant heating in the photothigmotron, the T_b at escape to the shade increased as substrate temperature increased.

10. Morning basking was a deliberate attempt to rapidly raise T_b from near burrow temperature to the T_b of the regulating phase. Almost all behavior during this phase was thermoregulatory, with minimum feeding and social behavior. The morning heating rate was, on the average, 3.3 times greater than the regulating phase heating rate and 4.0 times greater than the regulating phase cooling rate. Regulating phase heating, by behavioral, passive, and physiological means, was 1.15 times greater than cooling. Iguanas also heated faster than they cooled in a controlled environmental room. All heating and cooling rates were dependent on body weight, with a doubling of weight decreasing the morning heating rate by an average of 54 percent, the regulating phase heating rate by 59 percent, and the regulating phase cooling rate by 62 percent.

Core T_b nearly equilibrated with burrow temperature after a mean of only 19 percent of nightly submergence time. Movement was minimal in the burrow, yet a common decrease in the cooling rate

at a mean T_b of 34.4 C was probably due to a postural change, an increased adductive contact of the limbs with the trunk and tail.

Average maximum burrow depth correlated well with the region of nearly perfect, 24 hour, soil temperature stability. Burrows also provided an ambient temperature higher than surface temperatures during the night and during cold fronts. Seasonal variation in mean, burrow terminus temperature probably did not vary more than 4 C.

The iguana cooling rate in burrows was probably reduced somewhat during the prebreeding months, when a male and female sometimes shared the same burrow. Larger nocturnal aggregations did not occur in the field.

11. Preemergence movement, consisting of a stepwise crawl toward the burrow mouth, began up to 37 minutes prior to emergence in one individual. Iguanas usually only emerged when their T_b's would quickly rise above burrow temperature. Emergence was always delayed by medium to heavy overcast. However, on rare occasions (12.5 percent of observations) iguanas would emerge and stay out even though T_b did not rise appreciably above burrow temperature. Summer free-ranging iguanas, removed from their habitats for up to a day during transmitter implantation, all demonstrated a phase delay in emergence time after release, which gradually disappeared over the next several days. Presumably, their biological clock was re-entraining to the natural day length. Emergence was a two step process; the crawl from deep in the burrow, presumably initiated by a biological clock, and the actual emergence from near the burrow mouth after a preemergence pause, probably activated by a range of

light intensities reaching the iguana's eyes, an intensity nearly always corresponding to a high positive net heat transfer.

Once emergent, iguanas usually stayed out the full day. No adult submerged due to intolerably high surface temperatures, at least in monitored Semi-open Scrub and more densely vegetated areas. Submergences due to overcast and rainfall were also uncommon, as expected in a large, slow cooling ectotherm.

Activity time was tightly coupled to photoperiod. The mean seasonal decrease in activity time, 3 hours and 26 minutes, was almost identical to the seasonal decrease in photoperiod, 3 hours and 14 minutes. Activity time was not appreciably reduced relative to sunrise or sunset by the decreased water availability in the dry season. Seasonal change in submergence timing was slightly less well tied to the sunset time than emergence was to sunrise, since seasonal variation in access to heated sunlit areas late in the day was greater than access to morning basking platforms at the primary study site. Several examples of long term, significant differences in activity times between individuals were linked to differences in shade timing due to topographical variation between home ranges. Activity periods of dominant males in the field were longer than for females and subdominant males, due to their later submergence times. Activity time in the Gainesville pen was also directly related to body weight. However, unlike the field, emergence times were even more tightly coupled to body weight than submergence times. This difference was probably due to the enormously higher iguana density in the pen than in the field, and the consequent replacement of territories with a weight correlated peck order.

The range of emergence T_b's in the field, 6.1 C, was slightly less than the submergence range, 8.2 C. T_b independent emergence was more clearly demonstrated in the Gainesville pen, where iguana's emerged at T_b's as low as 15 C. T_b at submergence was an average of 10.3 C higher than at emergence. No penned individual could be enticed by an artificially warmed external environment to remain outside the shelters after light intensity had decreased to a low level.

12. Activity during the morning heating phase was essentially constant in rate and, thus, independent of increasing T_b. Iguanas were most easily scared back into their burrows during this time, the submergence distance being considerably less than burrow length. An abrupt increase in activity occurred when the first foray commenced. Although neither the duration nor the mean heating rate of the morning heating phase differed from February to October for equal weight iguanas, the mean T_b at the start of the first foray was significantly lower in February than October, perhaps an acclimatization to lower winter temperatures.

The major portion of the regulating phase consisted of a series of forays through the sun-shade mosaic, usually starting and ending at the present burrow of residence. Maximum activity occurred during the first foray. The activity distribution was unimodal during the cooler months of November and December and became steadily more bimodal toward midsummer, with the midday lull corresponding to maximum surface temperatures. Burrow excavation was usually restricted to the midday hours of 1000 to 1400, with short excavation periods alternating with short basking periods. High radiant input during

the basking periods may be the reason for the midday excavation timing, since excessive heat loss was prevented and the procedure could be completed quickly.

Arboreal activity probably served two thermoregulatory functions as well as the securing of leaves and fruits; the avoidance of high surface temperatures at midday in midsummer and the seeking out of warmer basking sites in the winter morning. On the average, T_b rose during arboreal feeding in October.

The effectiveness of cloud cover in reducing activity was greatest during midafternoon, with a lesser peak in effectiveness at the start of the first foray. It was least effective during the hour of morning maximum activity.

13. The mean distance traveled on clear or nearly clear days did not differ significantly between first, second, and third forays. The rate of travel declined on each successive foray, but again less than significantly. Foray length was not depressed by overcast time equal to or less than 45 percent of foray time. Iguanas simply stopped if the overcast period was of long duration, assuming a prostrate posture until the overcast cleared, then resumed travel. As a result of the delay, the mean rate of travel during forays was inversely correlated with overcast time. Forays only occurred over a 5.5 C mean T_b range, from 35.0 to 40.5 C. Foray length and mean rate of travel were independent of T_b over this range, except when overcast time was 30 percent or less. The mean rate of travel was then inversely related to T_b, since iguanas spent more time sitting in the shade avoiding overheating.

Iguanas were more eurythermal during the first than subsequent forays. T_b during second and subsequent forays usually both increased and decreased relative to the starting T_b, staying near the middle of the regulating phase range. Iguanas actively maintained upper and lower thermal buffer zones, entered only during infrequent long term activity in sun-exposed and deeply shaded areas.

14. The log of mean distance traveled per day was directly and linearly related to the log of the confinement area. Active time averaged only 1.8 percent of the emergent time in the summer Gainesville pen and was estimated to equal 7.5 percent of emergent time in the field, a reasonable estimate based on tracking observation. In a limited time-motion study in the pen, thermoregulatory movements took up an average of 43 percent of total active time. Movement was defined as body displacement in the horizontal plane and thus did not include lifting limbs off hot substrates and proportional changes in substrate contact and trunk symmetry relative to the sun. Individual thermoregulatory movements took considerably less time than feeding and social movements. The total number of thermoregulatory movements per day was probably inversely related to body size.

15. Ground feeding during February through October occurred at a significantly lower T_b than arboreal feeding, since iguanas did not climb bushes before the start of the first foray. Since Iverson (1977) observed morning basking without feeding in bushes in winter, the absence of arboreal feeding below a T_b of 35.7 C was not due to an inability to climb. Although iguanas fed on the ground at T_b's as low as 23.6 C in the Gainesville pen and 30.0 C in the field, both feeding rates and meal size were lower than at higher T_b's. Probably

arboreal feeding at low T_b was rare or absent due to disinclinations to feed and to stop morning basking, usually performed on the ground.

Defecation was possible over a wide range of T_b's, from 25.0 to probably 46.2 C. However, the range for undisturbed iguanas was smaller, 33.6-40.4 C. Defecation usually occurred once a day during the first foray.

Water was normally obtained from food. Nonetheless, iguanas could drink proficiently from free-standing sources. Drinking in field captives was restricted to high mean T_b, 38.2, probably due to a reluctance to break morning basking.

Expelling nasal salt gland secretion via sneezing occurred at a fairly uniform rate during the day and was primarily restricted to the regulating phase ($\bar{X}$ T_b = 37.7 C).

16. The thermoregulatory movements and postures of *Cyclura carinata* were illustrated and described. Major thermoregulatory behaviors were quantified in relation to changing T_b under different ambient thermal environments.

The most important behavioral means of T_b control was moving between sunlit and shaded areas. Shuttling resulted in a rapid reversal of the direction of T_b change and was most in evidence on the T_b records at the minimum and maximum T_b's of the regulating phase. Shuttling rate varied significantly between individuals in field cages and was directly and linearly related to T_b stability. Basking occurred over the full range of body temperatures, all the way to the maximum voluntary tolerance, 43.8 C; that is, throughout the regulating phase. Only once was T_b observed to rise above this temperature, to 44.0 C in a small male in obvious heat stress unable

to reach shade due to a large male blocking its path in the field cage. Heat gain postures were particularly common early and late in the day, when solar flux was low. Only 18.9 percent of daily direct sunlight time in the summer cages was distributed between 1000 and 1500. During maximum midday heat input, iguanas were quite selective in choosing shade with a low air temperature and a high wind velocity, a predictive process clearly tied to learning the thermal habitat, possible in a territorial animal which stayed for long periods in one area.

17. Iguanas in the photothigmotron maximized radiant heat input below the minimum voluntary tolerance and either abruptly or gradually decreased the input as the preferred T_b range was approached. Orientation of the long axis relative to the rays of the sun was coupled with trunk tilting. At low substrate temperature below the minimum voluntary tolerance, iguanas maximized the trunk exposure area on the side facing the sun by tilting the body away. This response was lost at higher substrate temperatures. Blindfolding eliminated sun orientation behavior. apparently mediated visually, but did not alter thigmothermic behavior.

Sun orientation changed daily and seasonally. Consistently predictable patterns of daily orientation were most in evidence at T_b and ambient environmental temperature extremes: positive parallel and positive perpendicular orientations during warming toward the preferred T_b range and negative parallel and perpendicular orientations during approach toward the maximum voluntary tolerance. The main heat gain orientations were positive perpendicular and positive parallel in summer and winter, respectively. The latter may have

been more effective in winter, when the sun declination was high, since foreleg elevation of the forebody not only reduced contact with the cold substrate but also brought the long axis of the body closer to a perpendicular angle with the incoming radiation. Object utilization was also more frequent during winter morning and evening basking. Negative parallel orientation, minimizing radiant heat gain from the sun, was more commonly seen during the summer than the winter.

Iguanas may preferentially heat their proximal colon, located on the left side of the anterior abdomen, by orienting that side toward the sun.

Patterns of travel during forays changed in a regular fashion during the February and October day. Iguanas most commonly moved clockwise during the morning (peak at 1000 to 1100), linearly at midday, and counterclockwise in the afternoon (maximum plateau between 1100 and 1500), probably visually keying the change to the movement of the sun across the sky.

The rate of heating of dried skin patches from various parts of the iguana's body increased faster posterior to the imbricate edges of the scales than anterior as the angle of incidence of the heat lamp radiation increased, especially for the more highly imbricated patches. Since the dorsal scale rows ran obliquely toward the mid-sagittal crest at an anterior angle of approximately 60°, iguanas should orient at greater than 90° to maximize heat input. This did appear to be the case, though more work is needed to be sure.

18. Iguanas deliberately changed their substrate contact by using neck, thoracic, abdominal, foreleg, and hindleg muscles to increase heat input

from the substrate or to avoid excessively hot substrates. Maximum substrate contact varied from approximately 13.4 to 16.0 percent of total surface area. Head-neck contact, foreleg participation, hindleg participation, and lateral compression accounted for maxima of 15, 48, 30, and 16 percent of maximum possible substrate contact, respectively.

T_a, T_s, and T_b all had an effect on the amount of substrate contact in a low, radiant heat exchange rate environment. A T_a greater than T_b and a T_s equally less than T_b resulted in low substrate contact and decreasing T_b. Conversely, a T_a less than T_b and T_s equally greater than T_b resulted in a high substrate contact and increasing T_b. Once in the preferred range in a cool air environment, substrate contact decreased even though T_s remained constant and above T_b. Thus, the iguana increased cool air contact to reduce further T_b rise. Iguanas were quite sensitive to small $T_s - T_b$ and $T_a - T_b$ differences.

During radiant heating in the photothigmotron, substrate contact only gradually increased as T_b increased, even when T_s was considerably higher than T_b. Since the same gradual relaxation was consistently observed in the field, especially during the morning heating phase, it may be a means of either maximizing radiant input while minimizing the normal heat loss to a cooler substrate, or of achieving a balance between radiant and thigmothermic heating. In fact, substrate contact in the photothigmotron was greater at higher substrate temperatures. However, the initial low body contact may also be due to greater wariness at low T_b, noted in the field. Holding the head higher off the ground increased the visual field, decreasing the chance of being caught unprepared for escape at a T_b where recovery from exercise occurred at a low rate.

Measurement of substrate temperature beneath maximally prostrate iguanas commonly revealed a small positive $T_b - T_s$ difference rather than the expected thigmothermia. Nonetheless, the rate of heat loss in this posture could easily be less than in a more upright posture due to decreased convective heat loss and probable localized ventral vasoconstriction. Also, the energy expenditure to maintain the prostrate posture was minimal.

19. Behavioral responses during cooling were lost in the order of decreasing neural pathway complexity. Lizards could still bloat below the CTMin, adaptive in that a nearly helpless iguana could wedge itself securely in its burrow or, perhaps, intimidate a predator. As expected, the CTMin, 12.5 C, was about equal to the lowest environmental temperature recorded during the study.

20. *Cyclura carinata* was a true panting lizard. At least five effector outputs probably increased proportionally above a panting threshold temperature; that is, gaping time per minute, degree of gape, extent of elevation and blood engourgement of the tongue, respiratory rate, and salivation rate. The function of panting is likely the cooling of the brain at high head temperature.

Eye bulging started soon before or soon after panting and was correlated with a reduction in the heating rate of the head at high head temperature. It probably also served directly as a means of removing ecdysing skin from around the eyes.

Head temperature was consistently higher than gut temperature during basking ($\bar{X}$ head-gut temperature = 1.0 C, range = -0.1 to 1.6 C), the head heating up to six times faster than the gut during one short, two-day monitoring period. Rapid head heating presents the

heliothermic, high T_b, ectotherm with an additional selective advantage for evolving a precise panting response and jugularis constriction.

The gut temperature at the panting threshold decreased from 32.8 C to above 43.8 C as the rate of heating increased. This is further circumstantial evidence for a panting regulator input from skin surface, temperature receptors. The panting time after shading was well correlated with the sum of gut and head temperature lag times, indicating that both temperatures may be important in sustaining panting.

The CTMax was approximately 46.2 C and the LM approximately 48.0 C. The minimum thermal safety margin was 4.8 C at midmorning, more than adequate for slow heating adults to avoid fatally overheating by finding shade.

21. Integumental reflectivity varied considerably over the body surface, being least labile and highest on the ventral tail and abdomen and lowest and quite labile on the dorsal surface. The change in reflectivity and coloration with increasing T_b probably served both concealment and thermoregulatory functions. The low reflectivity, dark phase characteristic of morning basking was well matched spectrally to the algal encrusted calcium carbonate substrates on which iguanas commonly basked. The initiation of the light phase, with its tinges of green and yellow evident in Water Cay iguanas, correlated well with the T_b range of the first foray into the sun-vegetational shade mosaic. The rate of heat gain in the light phase was estimated to be 15.3 percent less than in the dark phase under one set of defined thermal conditions.

The histology and distribution of integumental sensory spots suggests that they serve as mechanoreceptors. However, since jaw rubbing, sand swimming, and hard substrate rubbing with the ventral body surface all occurred in contexts suggesting substrate temperature detection, sensory spots may also be thermal receptors.

22. The mean, uncorrected conductance cooling/heating ratios in the cage and on the jig were 0.658 and 0.721, respectively. Iguanas always heated faster than they cooled, with a slightly but not significantly lower rate in the cage than on the jig. The jig ratio was at the low end of values reported for other lizards. Mean metabolic corrections of 62 and 67 percent of the maximum metabolic rate at 30 C were required to increase the C/H conductance ratios to one for iguanas on the jig and in the cage, respectively. Since this seems unrealistically high, *Cyclura* does appear to have some physiological thermoregulatory control, presumably via locally regulated, peripheral vasomotor control.

Climbing and walking in the cage and struggling on the jig occurred at significantly higher temperatures during heating than during cooling, corresponding to active avoidance of high and low T_b's, respectively. The same was true for defecation.

The respiratory rate was significantly greater during heating, perhaps due to thermal hysteresis, either between gut and brain temperatures or between gut and lung temperatures.

23. The log of the resting metabolic rate was directly and linearly related to T_b and was consistently above expectation, probably due to incomplete recovery from forced maximum exercise at the time of measurement. The log of maximum oxygen consumption vs. T_b was

best fitted to a second degree polynomial. The maximum rate occurred at 43-44 C, near the maximum voluntary tolerance. Maximum rates were similar to another fairly sluggish herbivore, *Sauromalus hispidus*, and lower than rates for the active carnivore, *Varanus gouldii*. The maximum rate of oxygen consumption was less thermally sensitive than the resting rate above 22.5 C, slightly below the T_b of emergence, reaching a Q_{10} one-half as large as 42 C. The factorial scope was also largest at slightly below emergence T_b, decreasing from about a maximum of six to about four in the mean preferred T_b range. As expected, maximum oxygen scope occurred at 38.1 C, slightly above preferred T_b.

24. The log of resting heart rate vs. T_b was fitted best by two straight lines meeting at 25.0 C. This commonly observed break occurred at a higher T_b than in more cold resistant lizard species. The log of maximum heart rate was fitted best to a second degree polynomial. The resting and maximum heart rate lines extrapolated to equality at 47.4 C, near the lethal maximum. Maximum heart rate was never more than 1.69 times the resting rate between 13.4 and 43.0 C. As expected, the heart rate increment maximized at 38.5 C, near the preferred T_b. Both resting and maximum exercise oxygen pulse declined between 13.4 and 43.0 C, by factors of 2.3 and 3.0, respectively. Thus, iguanas depended on increased heart rate rather than increased stroke volume and A-V difference to deliver the increased oxygen demand to the tissues as T_b increased. This contrasts to the low contribution of heart rate increase at any one T_b ($\bar{X}$ = 14.7 percent between 15 and 40 C using Gatten's 1974b equation) to the satisfaction of the increased oxygen demand during activity.

The high similarity between preferred T_b, 37.0 C, and T_b's for maximum heart rate increment, 38.5 C, maximum oxygen scope, 38.1 C, and maximum early rate of recovery from maximum exercise, 37.3 C, may in part be due to the high stenothermality of *Cyclura carinata*.

25. Maximum burst activity could be maintained for only the first thirty seconds during hand manipulation. Iguanas were practically helpless between feeble struggling bouts during the fourth to ninth minutes. They depended heavily on anaerobic metabolism to attain maximum activity, as indicated by the large oxygen debt. Iguanas recovered slowly from maximum exercise, requiring a mean of 82 to 118 minutes to reach the resting metabolic rate. Recovery occurred in the shortest time at a T_b of 25 C, followed by 15 and 20 C, 31 and 37 C, and finally, 42 C. The recovery rate increased as T_b increased, with the log of the overall recovery rate and the log of the rate during the first five minutes vs. T_b fitted best by second degree polynomials, and the log of the rate from minute 15 to full recovery fitted best by a straight line. The maximum rate of recovery during the first five minutes was well correlated with preferred T_b. This may be adaptive, since small oxygen debts were undoubtedly more common than large debts in the field. The alactacid debt averaged only 8.5 percent of the total debt (3.0-20.2 percent) and was practically T_b independent, whereas the lactacid debt averaged 91.5 percent of the total debt and increased curvilinearly with T_b. Overall, approximately the equivalent of the resting rate of metabolism was devoted to recovery from the oxygen debt, over and above resting metabolism devoted to other processes.

Strenuous activities were usually of short duration in the field, probably because recovery from extended maximum exercise was such a slow process. Walking was probably primarily an aerobic activity, based on its discontinuous nature and comparison of rates of travel with other lizards for which blood lactate levels were measured. More strenuous activities were also either discontinuous (climbing, digging) or of short duration and not soon repeated (copulations, escapes to burrows, male-male territorial chases). Two infrequent activities, nesting and male-male fights, probably did result in an oxygen debt. Protracted copulation, fighting, chases, and nesting in field cages and the Gainesville pen were followed by depressed activity for the rest of the day. The inability of iguanas to sustain burst activity for periods longer than 30 seconds, coupled with the ineffectuality of their static defense, were probably the main causes of their extirpation from Water Cay by dogs and feral cats.

REFERENCES

Aleksiuk, M. 1976. Reptilian hibernation: Evidence of adaptive strategies in *Thamnophis sirtalis parietalis*. Copeia 1976(1): 170-178.

Atkins, G. L. 1969. Multicompartment models for biological systems. Methuen and Co., Ltd., London. 153 p.

Auffenberg, W. A. The feeding strategy of *Cyclura carinata*. In prep.

Auth, D. L. 1975. Behavioral ecology of basking in the yellow-bellied turtle, *Chrysemys scripta scripta* (Schoepff). Bull. Fla. Sta. Mus. Biol. Sci. 20(10): 1-45.

Avery, D. F. 1976. Thermoregulation, metabolism, and social behavior in Lacertidae. p. 245-259. *In* A. d'A. Bellairs and C. B. Cox, eds., Morphology and biology of reptiles. Academic Press, London. 290 p.

_____. 1978. Activity patterns, thermoregulation and food consumption in two sympatric lizard species (*Podarcis muralis* and *P. sicula*) from central Italy. J. Anim. Ecol. 47(1): 143-158.

_____, and W. W. Tanner. 1971. Evolution of the iguanine lizards (Sauria, Iguanidae) as determined by osteological and myological characters. Brigham Young Univ. Sci. Bull. 12(3): 1-79.

Axtell, R. W. 1960. Orientation by *Holbrookia maculata* (Lacertilia, Iguanidae) to solar and reflected heat. Southwestern Natur. 5(1): 45-47.

Baharav, D. 1971. Movement ecology of the horned lizard *Phrynosoma solare*. Unpub. M.S. Thesis. Ariz. St. Univ., Tempe.

Bailey, S. E. R. 1969. The responses of sensory receptors in the skin of the green lizard, *Lacerta viridis*, to mechanical and thermal stimulation. Comp. Biochem. Physiol. 29(1): 161-172.

Baker, L. A., W. Weathers, and F. White. 1972. Temperature induced peripheral blood flow changes in lizards. J. Comp. Physiol. 80: 313-323.

Ballenger, R. E., J. Hawker, and O. J. Sexton. 1969. The effect of photoperiod acclimation on the thermoregulation of the lizard *Sceloporus undulatus*. J. Exp. Zool. 171(1): 43-48.

_____, and G. D. Schrank. 1970. Acclimation rate and variability of the critical thermal maximum in the lizard *Phrynosoma cornutum*. Physiol. Zool. 43(1): 19-22.

Barber, B. J. 1976. A theoretical and experimental analysis of behavioral temperature regulation in the lizard *Dipsosaurus dorsalis*. Ph.D. Thesis. Univ. Kentucky. 214 p. Univ. Microfilms Int. Ann Arbor Mich. (Diss. Abstr. 37(09): 4330B).

_____, and E. C. Crawford, Jr. 1977. A stochastic duel-limit hypothesis for behavioral thermoregulation in lizards. Physiol. Zool. 50(1): 53-60.

_____, and E. C. Crawford, Jr. 1979. Dual threshold control of peripheral temperature in the lizard *Dipsosaurus dorsalis*. Physiol. Zool. 52(3): 250-263.

Bartholomew, G. A. 1966. A field study of temperature relations in the Galapagos marine iguana. Copeia 1966(2): 241-250.

_____, A. F. Bennett, and W. R. Dawson. 1976. Swimming, diving, and lactate production of the marine iguana, *Amblyrhynchus cristatus*. Copeia 1976(4): 709-720.

_____, and R. C. Lasiewski. 1965. Heating and cooling rates, heart rates, and simulated living in the Galapagos marine iguana. Comp. Biochem. Physiol. 16(4): 573-582.

_____, and V. A. Tucker. 1963. Control of changes in body temperature metabolism, and circulation by the agamid lizard *Amphibolurus barbatus*. Physiol. Zool. 36(3): 199-218.

_____, and V. A. Tucker. 1964. Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards. Physiol. Zool. 37(4): 341-354.

_____, V. A. Tucker, and A. K. Lee. 1965. Oxygen consumption, thermal conductance, and heart rate in the Australian skink, *Tiliqua scincoides*. Copeia 1965(1): 169-173.

Bartlett, P. N. and D. M. Gates. 1967. The energy budget of a lizard on a tree trunk. Ecology 48(2): 315-322.

Bennett, A. F. 1972. The effect of activity on oxygen consumption, oxygen debt, and heart rate in the lizards *Varanus gouldii* and *Sauromalus hispidus*. J. Comp. Physiol. 79: 259-280.

_____. 1973. Blood physiology and oxygen transport during activity in two lizards, *Varanus gouldii* and *Sauromalus hispidus*. Comp. Biochem. Physiol. 46A(4): 673-690.

_____, and W. R. Dawson. 1972. Aerobic and anaerobic metabolism during activity in the lizard *Dipsosaurus dorsalis*. J. Comp. Physiol. 81: 289-299.

_____, and W. R. Dawson. 1976. Metabolism. Pp. 127-223. *In* C. Gans and W. R. Dawson, eds., Biology of the Reptilia, Vol. 5 (Physiology A). Academic Press, New York. 556 p.

Bennett, A. F. and T. T. Gleeson. 1976. Activity metabolism in the lizard *Sceloporus occidentalis*. Physiol. Zool. 49(1): 65-76.

_____, and P. Licht. 1972. Anaerobic metabolism during activity in lizards. J. Comp. Physiol. 81: 277-288.

_____, and P. Licht. 1974. Relative contributions of anaerobic and aerobic energy production during activity in amphibia. J. Comp. Physiol. 87: 351-360.

Berk, M. L. and J. E. Heath. 1975a. An analysis of behavioral thermoregulation in the lizard, *Dipsosaurus dorsalis*. J. Thermal Biol. 1(1): 15-22.

_____, and J. E. Heath. 1975b. Effects of preoptic, hypothalamic, and telencephalic lesions on thermoregulation in the lizard, *Dipsosaurus dorsalis*. J. Thermal Biol. 1(2): 65-78.

Berkson, H. 1966. Physiological adjustments to prolonged diving in the Pacific green turtle (*Chelonia mydas agassizii*). Comp. Biochem. Physiol. 18(1): 101-119.

Bernheim, H. A. and M. J. Kluger. 1976a. Fever and antipyresis in the lizard *Dipsosaurus dorsalis*. Amer. J. Physiol. 231(1): 198-203.

_____, and M. J. Kluger. 1976b. Fever: Effect of drug-induced antipyresis on survival. Science 193: 237-239.

Bligh, J. 1966. The thermosensitivity of the hypothalamus and thermoregulation in mammals. Biol. Rev. 41: 317-367.

_____. 1972. Neuronal models of mammalian temperature regulation. Pp. 105-120. *In* J. Bligh and R. E. Moore, eds., Essays on temperature regulation. North-Holland Publ. Co., Amsterdam. 186 p.

_____, and A. M. Harthoorn. 1965. Continuous radiotelemetric records of the deep body temperature of some unrestrained African mammals under near-natural conditions. J. Physiol. 176: 145-162.

_____, G. Louw, and B. A. Young. 1976. Effect of cerebro-ventricular administration of noradrenaline and carbochal on behavioral and autonomic thermoregulation in the monitor lizard *Varanus albigularis albigularis*. J. Thermal Biol. 1(4): 241-243.

_____, and R. E. Moore. 1972. Essays on temperature regulation. North-Holland Publ. Co., Amsterdam. 186 p.

Bogert, C. M. 1949a. Thermoregulation in reptiles, a factor in evolution. Evolution 3(1): 195-211.

Bogert, C. M. 1949b. Thermoregulation and eccritic body temperatures in Mexican lizards of the genus *Sceloporus*. An. Inst. Biol. Mex. 20: 415-426.

Bostic, D. L. 1966. Food and feeding behavior of the teiid lizard, *Cnemidophorus hyperthrus beldingi*. Herpetologica 22(1): 23-31.

Bradshaw, S. D. and A. R. Main. 1968. Behavioural attitudes and regulation of temperature in *Amphibolurus* lizards. J. Zool. London 154(2): 193-221.

Brattstrom, B. H. 1965. Body temperatures in reptiles. Amer. Midl. Nat. 73(2): 375-422.

_____. 1968. Thermal acclimation in anuran amphibians as a function of latitude and altitude. Comp. Biochem. Physiol. 24(1): 93-111.

_____. 1971. Social and thermoregulatory behavior of the bearded dragon, *Amphibolurus barbatus*. Copeia 1971(3): 484-497.

Brooks, G. R. 1968. Body temperatures of three lizards from Dominica, West Indies. Herpetologica 24(3): 209-214.

Brown, G. D. and T. J. Dawson. 1977. Seasonal variations in the body temperature of unrestrained kangaroos (Macropodidae: Marsupialia). Comp. Biochem. Physiol. 56A(1): 59-67.

Burns, T. A. 1971. Effect of temperature on heart and ventilatory rates of *Sceloporus jarrovi*. Southwestern Nat. 15(4): 465-471.

Bustard, R. H. 1970. The role of behavior in the natural regulation of numbers in the Gekkonid lizard *Gehydra variegata* (Dumeril and Bibron). Ecology 51(4): 724-728.

Cabanac, M. and H. T. Hammel. 1971. Comportement thermoregulateur du lezard *Tiliqua scincoides*. Responses au froid. J. Physiol. Paris 63: 222-225.

_____, H. T. Hammel, and J. D. Hardy. 1967. *Tiliqua scincoides:* Temperature-sensitive units in lizard brain. Science 158: 1050-1051.

_____, J. A. J. Stolwijk, and J. D. Hardy. 1968. Effect of temperature and pyrogens on single-unit activity in the rabbit's brain stem. J. Appl. Physiol. 24: 645-652.

Campbell, H. W. 1969. The effect of temperature on the auditory sensitivity of lizards. Physiol. Zool. 42(2): 183-210.

Carey, W. M. 1975. The rock iguana, *Cyclura pinguis*, on Anegada British Virgin Islands, with notes on *Cyclura ricordi* and *Cyclura cornuta* on Hispaniola. Bull. Fla. Sta. Mus. Biol. Sci. 19(4): 189-233.

Carpenter, C. C. 1966. The marine iguana (*Amblyrhynchus cristatus*) of the Galapagos Islands, its behavior and ecology. Proc. Calif. Acad. Sci 34(6): 329-375.

_____. 1969. Behavioral and ecological notes on the Galapagos land iguanas. Herpetologica 25(3): 155-164.

Case, T. J. 1976. Seasonal aspects of thermoregulatory behavior in the chuckwalla, *Sauromalus obesus* (Reptilia, Lacertilia, Iguanidae). J. Herpetol. 10(2): 84-95.

_____. 1978. A general explanation for insular body size trends in terrestrial vertebrates. Ecology 59(1): 1-18.

Chong, G., H. Heatwole, and B. T. Firth. 1973. Panting thresholds of lizards II. Diel variation in the panting threshold of *Amphibolurus muricatus*. Comp. Biochem. Physiol. 46A(4): 827-829.

Clark, D. R. and J. C. Kroll. 1974. Thermal ecology of anoline lizards: Temperate vs. tropical strategies. Southwestern Nat. 19(1): 9-19.

Clark, R. F. 1965. An ethological study of the iguanid lizard genus *Callisaurus*, *Cophosaurus*, and *Holbrookia*. Emporia Sta. Res. Stud. 13: 1-66.

Cogger, H. G. 1974. Thermal relations of the malle dragon, *Amphibolurus fordi* (Lacertilia: Agamidae). Aust. J. Zool. 22(3): 319-339.

_____, and A. Holmes. 1960. Thermoregulatory behavior in a specimen of *Morelia variegata* Gray (Serpentes: Boidae). Proc. Linn. Soc. N.S.W. 85: 328-333.

Corn, M. J. 1971. Upper thermal limits and thermal preferenda for three sympatric species of *Anolis*. J. Herpetol. 5(1-2): 17-21.

Cowles, R. B. and C. M. Bogert. 1944. A preliminary study of thermal requirements of desert reptiles. Bull. Amer. Mus. Nat. Hist. 83: 265-296.

_____, and G. L. Burleson. 1944. The sterilizing effect of high temperatures on the male germ plasm of the yucca night-lizard, *Xantusia vigilis*. Amer. Nat. 79: 417-435.

Crawford, E. C. Jr. 1972. Brain and body temperature in a panting lizard. Science 177: 431-433.

_____, and B. J. Barber. 1974. Effects of core, skin, and brain temperature on panting in the lizard *Sauromalus obesus*. Amer. J. Physiol. 226(3): 569-573.

Crawford, E. C. Jr., J. Palomeque, and B. J. Barber. 1977. A physiological basis for head-body temperature differences in a panting lizard. Comp. Biochem. Physiol. 56A: 161-163.

Cunningham, J. D. 1966. Thermal relations of the alligator lizard *Gerrhonotus multicarinatus webbi*. Herpetologica 22(1): 1-7.

Dawson, W. R. 1967. Interspecific variation in physiological responses of lizards to temperature. Pp. 230-257. *In* W. W. Milstead, ed., Lizard ecology: A symposium. Univ. Missouri Press, Columbia, Mo. 300 p.

_____. 1975. On the physiological significance of the preferred body temperatures of reptiles. Pp. 443-473. *In* D. M. Gates and R. B. Schmerl, eds., Perspectives of biophysical ecology. Ecol. Studies, Vol. 12. Springer-Verlag, New York. 609 p.

Depocas, F. and J. S. Hart. 1957. Use of the Pauling oxygen analyzer for measurement of oxygen consumption of animals in open-circuit systems and in a short-lag, closed-circuit apparatus. J. Appl. Physiol. 10: 388-392.

DeWitt, C. B. 1963. Behavioral thermoregulation in the iguanid lizard *Dipsosaurus dorsalis*. Ph.D. Thesis. Univ. Michigan. 92 p. Univ. Microfilms Int. Ann Arbor, Mich. (Diss. Abstr. 25(4): 2670).

_____. 1967. Precision of thermoregulation and its relation to environmental factors in the desert iguana, *Dipsosaurus dorsalis*. Physiol. Zool. 40(1): 49-66.

_____, and R. M. Friedman. 1979. Significance of skewness in ectotherm thermoregulation. Amer. Zool. 19(1): 195-209.

Dial, B. E. 1978. The thermal ecology of two sympatric nocturnal *Coleonyx* (Lacertilia: Gekkonidae). Herpetologica 34(2): 194-201.

Dmi'el, R. and D. Rappeport. 1976. Effect of temperature on metabolism during running in the lizard *Uromastix aegyptius*. Physiol. Zool. 49(1): 77-84.

Dunson, W. A. 1976. Salt glands in reptiles. Pp. 413-445. *In* C. Gan and W. R. Dawson, eds., Biology of the reptilia, Vol. 5 (Physiology A). Academic Press, New York. 556 p.

Eisenman, J. S. 1969. Pyrogen-induced changes in the thermosensitivity of septal and preoptic neurons. Amer. J. Physiol. 216(2): 330-334.

Ellis, H. I. and J. P. Ross. 1978. Field observations of cooling rates of Galapagos land iguanas (*Conolophus subcristatus*). Comp. Biochem Physiol. 59A(2): 205-209.

Feder, M. E. 1976. Oxygen consumption and body temperature in neotropical and temperate zone lungless salamanders (Amphibia: Plethodontidae). J. Comp. Physiol. 110: 197-208.

_____. 1978. Environmental variability and thermal acclimation in neotropical and temperate zone salamanders. Physiol. Zool. 51(1): 7-16.

Fitch, H. S. 1954. Life history and ecology of the five-lined skink, *Eumeces fasciatus*. Univ. Kans. Publ. Mus. Nat. Hist. 8: 1-156.

_____. 1960. Autecology of the copperhead. Univ. Kans. Publ. Mus. Nat. Hist. 13: 85-288.

_____. 1972. Ecology of *Anolis tropidolepis* in Costa Rican cloud forest. Herpetologica 28(1): 10-21.

_____. 1973. A field study of Costa Rican lizards. Univ. Kans. Sci. Bull. 50(2): 39-126.

Fitzpatrick, L. C., J. L. Hughes, and B. J. Venables. 1978. Relations between preferred body temperatures and metabolic compensation in the rusty lizard, *Sceloporus olivaceous*. Comp. Biochem. Physiol. 59A(1): 13-16.

Fox, W., C. Gordon, and M. Fox. 1961. Morphological effects of low temperatures during the embryonic development of the garter snake, *Thamnophis elegans*. Zoologica 46: 57-71.

Garrick, L. D. 1974. Reproductive influences on behavioral thermoregulation in the lizard *Sceloporus cyanogenys*. Physiol. and Behav. 12: 85-91.

_____. 1979. Lizard thermoregulation: Operant responses for heat at different thermal intensities. Copeia 1979(2): 258-266.

Gatten, R. E. Jr. 1974a. Effects of temperature and activity on aerobic and anaerobic metabolism and heart rate in the turtles *Pseudemys scripta* and *Terrapene ornata*. Comp. Biochem. Physiol. 48A(4): 619-648.

_____. 1974b. Percentage contribution of increased heart rate to increased oxygen transport during activity in *Pseudemys scripta*, *Terrepene ornata*, and other reptiles. Comp. Biochem. Physiol. 48A(4): 649-652.

_____. 1974c. Effect of nutritional status on the preferred body temperature of the turtles *Pseudemys scripta* and *Terrapene ornata*. Copeia 1974(4): 912-917.

_____. 1978. Aerobic metabolism in snapping turtles, *Chelydra serpentina*, after thermal acclimation. Comp. Biochem. Physiol. 61A(3): 325-337.

Geiger, R. 1957. The climate near the ground. Harvard Univ. Press, Cambridge, Mass. 494 p.

Gelderloos, Orin G. 1976. Circadian activity patterns in the desert iguana, *Dipsosaurus dorsalis*. Physiol. Zool. 49(1): 100-108.

Gratz, R. K. and V. H. Hutchison. 1977. Energetics for activity in the diamondback water snake *Natrix rhombifera*. Physiol. Zool. 50(2): 99-114.

Greenberg, N. 1976. Thermoregulatory aspects of behavior in the blue spiny lizard *Sceloporus cyanogenys* (Sauria, Iguanidae). Behavior 59(1-2): 1-21.

_____. 1977. An ethogram of the blue spiny lizard, *Sceloporus cyanogenys* (Reptilia, Lacertilia, Iguanidae). J. Herpetol. 11(2): 177-195.

Grenot, C. 1976. Ecophysiologie du lézard saharien *Uromastix acanthinurus* Bell, 1825 (Agamidae, herbivore). E'cole Normale Supérieure Publ. du Laboratoire de Zool. 7: 1-322.

Hammel, H. T. 1965. Neurons and temperature regulation. Pp. 71-98. *In* W. S. Yamamoto and J. R. Brobeck, eds., Physiological controls and regulations. Saunders, Philadelphia. 362 p.

_____, F. T. Caldwell, and R. M. Abrams. 1967. Regulation of body temperature in the blue-tongued lizard. Science 156: 1260-1262.

Hardy, D. F. 1962. The ecology and behavior of the six-lined racerunner, *Cnemidophorus sexlineatus*. Univ. Kans. Sci. Bull. 43: 3-73.

Harestad, A. S. and F. L. Bunnell. 1979. Home range and body weight--a reevaluation. Ecology 60(2): 389-402.

Harlow, H. J., S. S. Hillman, and M. Hoffmann. 1976. The effect of temperature on digestive efficiency in the herbivorous lizard, *Dipsosaurus dorsalis*. J. Comp. Physiol. 111: 1-6.

Heath, J. E. 1964. Head-body temperature differences in horned lizards. Physiol. Zool. 37(3): 273-279.

_____. 1965. Temperature regulation and diurnal activity in horned lizards. Univ. Cal. Publ. Zool. 64(3): 97-136.

_____. 1966. Venous shunts in the cephalic sinuses of horned lizards. Physiol. Zool. 39(1): 30-35.

_____. 1970. Theory of behavioral regulation of temperature in poikilotherms. The Physiologist 13: 399-410.

Heatwole, H. 1970. Thermal ecology of the desert dragon *Amphibolurus inermis*. Ecol. Monogr. 40(4): 425-457.

Heatwole, H. 1976. Reptile ecology. Univ. Queensland Press, St. Lucia. 178 p.

_____, B. T. Firth, and H. Stoddart. 1975. Influence of season, photoperiod, and thermal acclimation on the panting threshold of *Amphibolurus maricatus*. J. Exp. Zool. 191(2): 183-192.

_____, B. T. Firth, and G. J. W. Webb. 1973. Panting thresholds of lizards I. Some methodological and internal influences on the panting threshold of the agamid, *Amphibolurus maricatus*. Comp. Biochem. Physiol. 46A(4): 799-826.

_____, T. Lin, E. Villalón, A. Muñiz, and A. Matta. 1969. Some aspects of the thermal ecology of Puerto Rican anoline lizards. J. Herpetol. 3(1-2): 65-77.

Heckrotte, C. 1967. Relations of body temperature, size, and crawling speed of the common garter snake, *Thamnophis s. sirtalis*. Copeia 1967(4): 759-763.

Heinrich, B. 1977. Why have some animals evolved to regulate a high body temperature? Amer. Nat. 111(980): 623-640.

Hennig, C. W. and W. P. Dunlap. 1978. Tonic immobility in *Anolis carolinensis*: Effects of time and conditions of captivity. Behav. Biol. 23(1): 75-86.

Hertz, P. E. 1974. Thermal passivity of a tropical forest lizard, *Anolis polylepis*. J. Herpetol. 8(4): 323-327.

Hirth, H. F. 1963. Some aspects of the natural history of *Iguana iguana* on a tropical strand. Ecology 44(3): 613-615.

_____. 1964. Temperature preferences of five species of neotropical lizards. Herpetologica 20(4): 273-276.

_____, and A. C. King. 1969. Body temperatures of snakes in different seasons. J. Herpetol 3(1-2): 101-102.

Huey, R. B. 1974. Winter thermal ecology of the iguanid lizard *Tropidurus peruvianus*. Copeia 1979(1): 149-155.

_____, and M. Slatkin. 1976. A cost-benefit model of lizard thermoregulation. Quart. Rev. Biol. 51(3): 363-384.

Hutchison, V. H., H. G. Dowling, and A. Vinegar. 1966. Thermoregulation in a brooding female Indian python, *Python molurus bivittatus*. Science 151: 694-696.

_____, and J. L. Larimer. 1960. Reflectivity of the integuments of some lizards from different habitats. Ecology 41(2): 199-209.

Hutchison, V. H., and J. D. Maness. 1978. The role of behavior in temperature acclimation and tolerance in ectotherms. Amer. Zool. 19: 367-381.

_____, L. D. Turney, and R. K. Gratz. 1977. Aerobic and anaerobic metabolism during activity in the salamander *Ambystoma tigrinum*. Physiol. Zool. 50(2): 189-202.

Iggo, A. 1969. Cutaneous thermoreceptors in primates and subprimates. J. Physiol. 200: 403-430.

_____. 1970. Somesthetic sensory mechanisms. *In* M. J. Swenson, ed., Duke's physiology of domestic animals. Cornell Univ. Press, Ithaca, New York. 949 p.

Inger, R. F. 1959. Temperature responses and ecological relations of two Bornean lizards. Ecology 40(1): 127-136.

Irwin, L. N. 1965. Diel activity and social interaction of the lizard *Uta stansburiana stejnegeri*. Copeia 1: 99-101.

Iverson, J. B. 1977. Behavior and ecology of the rock iguana, *Cyclura carinata*. Ph.D. Thesis. Univ. Florida. 379 p. Univ. Microfilms Int. Ann Arbor, Mich. (Diss. Abstr. 38(07): 3082B-3083B).

_____. 1979. Behavior and ecology of the rock iguana *Cyclura carinata*. Bull. Fla. Sta. Mus. Biol. Sci. 24(3): 175-358.

_____. 1980. Colic modifications in Iguanine lizards. J. Morph.

Jaburek, L. 1926. Über Nervenendigungen in der Epidermis der Reptilien. Zeit. M. Anal. Forsch. 10: 1-49.

Janzen, D. H. 1973. Sweep samples of tropical foliage insects: Effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54(3): 687-708.

Johnson, C. R. 1972. Head-body temperature differences in *Varanus gouldii* (Sauria: Varanidae). Comp. Biochem. Physiol. 43A(4): 1025-1029.

Johnson, S. R. 1965. An ecological study of the chuckwalla, *Sauromalus obesus* Baird, in the western Mojave Desert. Amer. Mid. Nat. 73(1): 1-29.

Judd, F. W. 1975. Activity and thermal ecology of the keeled earless lizard, *Holbrookia propinqua*. Herpetologica 31(2): 137-150.

Kennedy, J. P. 1968. Observations on the ecology and behavior of *Cnemidophorus guttatus* and *Cnemidophorus deppei* (Sauria, Teiidae) in Southern Veracruz. J. Herpetol. 2(3): 87-96.

Kennerly, T. E. 1964. Micro-environmental conditions of the pocket gopher burrow. Texas J. Sci. 16(4): 395-441.

Kenton, B., L. Kruger, and M. Woo. 1971. Two classes of slowly adapting mechanoreceptor fibers in reptile cutaneous nerve. J. Physiol. 212(1): 21-44.

Kluger, M. J. 1979. Fever in ectotherms: Evolutionary implications. Amer. Zool. 19(1): 295-304.

_____, D. A. Ringler, and M. R. Anver. 1975. Fever and survival. Science 188: 166-168.

_____, R. S. Tarr, and J. E. Heath. 1973. The effect of posterior hypothalamic lesions on thermoregulation in the lizard, *Dipsosaurus dorsalis*. Physiol. Zool. 46(1): 79-84.

Köppen, W. 1923. Die Klimate der Erde; Grundriss der Klimakunde. Walter de Gruyter Co., Berlin. 369 p.

Kosh, R. J. and V. H. Hutchison. 1968. Daily rhythmicity of temperature tolerance in Eastern painted turtles, *Chrysemys picta*. Copeia 1968(2): 244-246.

Kour, E. L. and V. H. Hutchison. 1970. Critical thermal tolerances and heating and cooling rates of lizards from diverse habitats. Copeia 1970(2): 219-229.

Krekorian, C. O., V. J. Vance, and A. M. Richardson. 1968. Temperature-dependent maze learning in the desert iguana, *Dipsosaurus dorsalis*. Anim. Behav. 16(4): 429-436.

Larson, M. W. 1961. The critical thermal maximum of the lizard *Sceloporus occidentalis* Baird and Girard. Herpetologica 17(2): 113-122.

Lee, A. K. and J. A. Badham. 1963. Body temperature, activity, and behavior of the agamid lizard, *Amphibolurus barbatus*. Copeia 1963(2): 387-394.

Licht, P. 1965a. Effects of temperature on heart rates of lizards during rest and activity. Physiol. Zool. 38(2): 129-137.

_____. 1965b. The relation between preferred body temperatures and testicular heat sensitivity in lizards. Copeia 1965(4): 428-436.

_____. 1968. Response of the thermal preferendum and heat resistance to thermal acclimation under different photoperiods in the lizard *Anolis carolinensis*. Am. Midl. Nat. 79(1): 149-158.

_____, and S. L. Basu. 1967. Influence of temperature on lizard testes. Nature 213: 672-674.

Licht, P., W. R. Dawson, V. H. Shoemaker, and A. R. Main. 1966. Observations on the thermal relations of western Australian lizards. Copeia 1966(1): 97-110.

_____, and W. R. Moberly. 1965. Thermal requirements for embryonic development in the tropical lizard *Iguana iguana*. Copeia 1965 (4): 515-517.

Lipton, J. M. 1971. Thermal stimulation of the medulla alters behavioral temperature regulation. Brain Res. 26(2): 433.

Lowe, C. H. and V. J. Vance. 1955. Acclimation of the critical thermal maximum of the reptile *Urosaurus ornatus*. Science 122: 73-74.

Mackay, R. S. 1964. Galapagos tortoise and marine iguana deep body temperatures measured by radio-telemetry. Nature 204: 355-358.

_____. 1968. Observations on peristaltic activity vs. temperature and circadian rhythms in undisturbed *Varanus flavescens* and *Ctenosaura pectinata*. Copeia 1968(2): 252-259.

_____. 1970. Bio-medical telemetry, 2nd ed. John Wiley and Sons, Inc., New York. 533 p.

Maderson, P. F. A. 1968. Observations on the epidermis of the tautara (*Sphenodon punctatus*). J. Anat. 103(2): 311-320.

Margaria, R., H. T. Edwards, and D. B. Dill. 1933. The possible mechanisms of contracting and paying the oxygen debt and the role of lactic acid in muscular contraction. Amer. J. Physiol. 106: 689-715.

Mauer, F. 1895. Die Epidermis und ihre Abkommlinge. Wilhelm Englemann, Leipzig. 352 p.

Mayhew, W. W. 1961. Photoperiodic response of female fringe-toe lizards. Science 134: 2104-2105.

_____. 1963. Temperature preferences of *Sceloporus orcutti*. Herpetologica 18(4): 217-233.

_____. 1964. Photoperiodic responses of three species of the lizard genus *Uma*. Herpetologica 20(2): 95-113.

McDonald, H. S. 1976. Methods for the physiological study of reptiles, Pp. 19-126. *In* C. Gans and W. R. Dawson, eds., Biology of the Reptilia, Vol. 5 (Physiology A). Academic Press, New York. 556 p.

McGinnis, S. M. 1966. *Sceloporus occidentalis*: Preferred body temperature of the western fence lizard. Science 152: 1090-1091.

_____. 1970. Flexibility of thermoregulatory behavior in the western fence lizard *Sceloporus occidentalis*. Herpetologica 26(1): 70-76.

McGinnis, S. M. and C. W. Brown. 1966. Thermal behavior of the green iguana, *Iguana iguana*. Herpetologica 22(3): 189-199.

_____, and L. L. Dickson. 1967. Thermoregulation in the desert iguana, *Dipsosaurus dorsalis*. Science 156: 1757-1759.

McManus, J. J. and D. W. Nellis. 1973. Temperature and metabolism of a tropical lizard, *Anolis acutus*. Comp. Biochem. Physiol. 45A(2): 403-410.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. Amer. Nat. 97: 133-140.

_____. 1966. The metabolism of fossorial rodents: A study of convergence. Ecology 47(5): 712-733.

_____, and W. Auffenberg. 1976. The effect of large body size on the temperature regulation of the Komodo Dragon, *Varanus komodoensis*. Comp. Biochem. Physiol. 55A(4): 345-350.

Meyer, B. S. and D. B. Anderson. 1952. Plant physiology. D. Van Nostrand Co., Inc., Princeton, New Jersey. 784 p.

Miller, M. R. and M. Kasahara. 1967. Studies on the cutaneous innervation of lizards. Proc. Calif. Acad. Sci. 34: 549-568.

Mills, F. C. 1955. Statistical methods, 3rd ed. Holt, Rinehart, and Winston, New York. 842 p.

Moberly, W. R. 1968. The metabolic responses of the common iguana, *Iguana iguana*, to walking and diving. Comp. Biochem. Physiol. 27(1): 21-32.

Morgareidge, K. R. and F. N. White. 1969. Cutaneous vascular changes during heating and cooling in the Galapagos marine iguana. Nature 223: 587-591.

Mueller, C. F. 1970. Temperature acclimation in two species of *Sceloporus*. Herpetologica 26(1): 83-85.

Murrish, E. E. and K. Schmidt-Nielsen. 1970. Exhaled air temperature and water conservation in lizards. Res. Physiol. 10: 151-158.

Muth, A. 1977a. Body temperatures and associated postures of the zebra-tailed lizard, *Callisaurus draconoides*. Copeia 1977(1): 122-125.

_____. 1977b. Thermoregulatory postures and orientation to the sun: A mechanistic evaluation for the zebra-tailed lizard, *Callisaurus draconoides*. Copeia 1977(4): 710-720.

Myhre, K. and H. T. Hammel. 1969. Behavioral regulation of internal temperature in the lizard *Tiliqua scincoides*. Amer. J. Physiol. 217(5): 1490-1495.

Myres, B. C. and M. M. Eells. 1968. Thermal aggregation in boa constrictor. Herpetologica 24(1): 61-66.

Nagy, K. A. 1973. Behavior, diet, and reproduction in the desert lizard, *Sauromalus obesus*. Copeia 1973(1): 93-102.

Nakayama, T., H. T. Hammel, J. D. Hardy, and J. S. Eisenman. 1963. Thermal stimulation of electrical activity of single units of the preoptic region. Amer. J. Physiol. 204: 1122.

Necker, R. 1974. Dependence of mechanoreceptor activity on skin temperature in sauropsids, I. *Caiman*. J. Comp. Physiol. 92: 65-73.

Norris, K. S. 1953. The ecology of the desert iguana, *Dipsosaurus dorsalis*. Ecology 34(2): 265-287.

_____. 1967. Color adaptations in desert reptiles and its thermal relationships. Pp. 162-229. *In* W. W. Milstead, ed., Lizard ecology: A symposium. Univ. Missouri Press, Columbia, Mo. 300 p.

Osgood, W. S. and P. D. Weigl. 1972. Monitoring activity of small mammals by temperature-telemetry. Ecology 53(4): 738-740.

Parker, W. S. and E. R. Pianka. 1973. Notes on the ecology of the iguanid lizard, *Sceloporus magister*. Herpetologica 29(2): 143-152.

_____, and E. R. Pianka. 1974. Further ecological observations on the western banded gecko, *Coleonyx variegatus*. Copeia 1974(2): 125-142.

Parmenter, C. J. and H. Heatwole. 1975. Panting thresholds of lizards IV. The effect of dehydration on the panting threshold of *Amphibolurus muricatus*. J. Exp. Zool. 191(3): 327-332.

Parry, D. A. 1951. Factors determining the temperature of terrestrial arthropods in sunlight. J. Exp. Biol. 28(3): 445-462.

Patterson, J. W. and P. M. C. Davies. 1978. Preferred body temperature: Seasonal and sexual differences in the lizard *Lacerta vivipara*. J. Thermal Biol. 3(4): 39-41.

Pearson, E. S. and H. O. Hartley. 1966. Biometrika tables for statisticians, Vol. 1. Cambridge Univ. Press. 264 p.

Pearson, O. P. 1954. Habits of the lizard, *Liolaemus multiformis multiformis*, at high altitudes in Southern Peru. Copeia 1954(2): 111-116.

_____. 1977. The effect of substrate and of skin color on thermoregulation of a lizard. Comp. Biochem. Physiol. 58A(4): 353-358.

Pentecost, E. D. 1974. Behavior of *Eumeces laticeps* exposed to a thermal gradient. J. Herpetol. 8(2): 169-173.

Pianka, E. R. 1969. Sympatry of desert lizards (*Ctenotus*) in Western Australia. Ecology 50(6): 1012-1030.

_____. 1971a. Comparative ecology of two lizards. Copeia 1971(1): 129-138.

_____. 1971b. Ecology of the agamid lizard *Amphibolurus isolepis* in Western Australia. Copeia 1971(3): 527-536.

_____. 1973. The structure of lizard communities, Pp. 53-74. *In* R. F. Johnston, P. W. Frank, and C. D. Michener, eds., Annual review of ecology and systematics, Vol. 3. Annual Reviews Inc., Palo Alto, California. 422 p.

_____, and W. S. Parker. 1972. Ecology of the iguanid lizard *Callisaurus draconoides*. Copeia 1972(3): 493-508.

_____, and W. S. Parker. 1975. Ecology of horned lizards: A review with special references to *Phrynosoma platyrhinos*. Copeia 1975(1): 141-162.

_____, and H. D. Pianka. 1970. The ecology of *Moloch horridus* (Lacertilia: Agamidae) in Western Australia. Copeia 1970(1): 90-103.

_____, and H. D. Pianka. 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian Desert. Copeia 1976(1): 125-142.

Porter, K. R. 1972. Herpetology. W. B. Saunders Co., Philadelphia. 524 p.

Porter, W. P. 1967. Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles. Ecol. Monogr. 37(4): 273-296.

_____, and D. M. Gates. 1969. Thermodynamic equilibria of animals with environment. Ecol. Monogr. 39(3): 245-270.

_____, and F. C. James. 1979. Behavioral implications of mechanistic ecology II: The African rainbow lizard, *Agama agama*. Copeia 1979(4): 594-619.

_____, J. W. Mitchell, W. A. Beckman, and C. B. DeWitt. 1973. Behavioral implications of mechanistic ecology. Thermal and behavioral modeling of desert ectotherms and their micro-environment. Oecologia 13: 1-54.

Pough, F. H. 1973. Lizard energetics and diet. Ecology 54(4): 837-844.

Pough, F. H. 1977. Ontogenetic change in blood oxygen capacity and maximum activity in garter snakes (*Thamnophis sirtalis*). J. Comp. Physiol. 114: 337-345.

_____, and W. N. McFarland. 1976. A physical basis for head-body temperature differences in reptiles. Comp. Biochem. Physiol. 53A(3): 301-303.

Precht, H. 1973. Limiting temperatures of life functions, Pp. 400-440. *In* H. Precht, J. Christophersen, H. Hensel, and W. Larcher, eds., Temperature and life. Springer-Verlag, New York. 779 p.

Prestrude, A. M. and F. T. Crawford. 1970. Tonic immobility in the lizard, *Iguana iguana*. Anim. Behav. 18(2): 391-395.

Prine, G. M. 1977. Agronomy research report AG 77-4. Agr. Exp. Sta., Univ. Florida. 13 p.

Ralph, C. L., B. T. Firth, and J. S. Turner. 1979. The role of the pineal body in ectotherm thermoregulation. Amer. Zool. 19(1): 273-293.

Rand, A. S. 1964. Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. Ecology 45(4): 863-864.

Rautenberg, W. 1969. Die Bedeutung der Zentralnervösen Thermosensitivitat für die Temperatur Regulation der Taube. Z. Vergleich. Physiol. 62: 235-266.

Regal, P. J. 1966. Thermophilic responses following feeding in certain reptiles. Copeia 1966(3): 588-590.

_____. 1967. Voluntary hypothermia in reptiles. Science 155: 1551-1553.

_____. 1968. An analysis of heat-seeking in a lizard. Ph.D. Thesis. U.C.L.A. 152 p. Univ. Microfilms Int. Ann Arbor, Mich. (Diss. Abstr. 29(11): 4447B).

_____. 1971. Long term studies with operant conditioning techniques of temperature regulation patterns in reptiles. J. Physiol. Paris 63: 403-406.

_____. 1975. The evolutionary origin of feathers. Quart. Rev. Biol. 50(1): 35-66.

Remington, R. D. and M. A. Schork. 1970. Statistics with applications to the biological and health sciences. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 418 p.

Richards, S. A. 1970. The biology and comparative physiology of thermal panting. Biol. Rev. 45: 223-264.

Rose, F. L. and F. W. Judd. 1975. Activity and home range size of the Texas tortoise, *Gopherus berlandieri*, in South Texas. Herpetologica 31(4): 448-456.

Roth, J. J. and C. L. Ralph. 1976. Body temperature of the lizard (*Anolis carolinensis*): Effect of parietalectomy. J. Exp. Zool. 198(1): 17-28.

_____, and C. L. Ralph. 1977. Thermal and photic preferences in intact and parietalectomized *Anolis carolinensis*. Behav. Biol. 19(3): 341-348.

Ruben, J. A. 1976. Reduced nocturnal heat loss associated with ground litter burrowing by the California red-sided garter snake *Thamnophis sirtalis infernalis*. Herpetologica 32(3): 323-325.

Ruibal, R. 1961. Thermal relations of five species of tropical lizards. Evolution 15(1): 98-111.

_____, and R. Philcbosian. 1970. Eurythermy and niche expansion in lizards. Copeia 1970(4): 645-653.

Schall, J. J. 1977. Thermal ecology of five sympatric species of *Cnemidophorus* (Sauria: Teiidae). Herpetologica 33(3): 261-272.

Schmidt-Nielsen, K., K. A. Borut, P. Lee, and E. C. Crawford, Jr. 1963. Nasal salt excretion and the possible function of the cloaca in water conservation. Science 142: 1300-1301.

_____, B. Schmidt-Nielsen, S. A. Jarnum, and T. R. Houpt. 1957. Body temperature of the camel and its relation to water economy. Amer. J. Physiol. 188: 103-112.

Schoener, T. W. 1968. Sizes of feeding territories among birds. Ecology 49(1): 123-141.

Schwalm, P. A., P. H. Starrett, and R. W. McDiarmid. 1977. Infrared reflectance in leaf-sitting neotropical frogs. Science 196: 1225-1227.

Seymour, R. S. 1973. Physiological correlates of forced activity and burrowing in the spadefoot toad, *Scaphiopus hammondii*. Copeia 1973(1): 103-115.

Shine, R. 1971. The ecological energetics of the scincid lizard *Egernia cunninghami* (Gray 1832). Unpub. Hons. Thesis, Australian Nat. Univ. Canberra.

Smith, E. N. 1976. Heating and cooling rates of the American alligator, *Alligator mississippiensis*. Physiol. Zool. 49(1): 37-48.

_____. 1979. Behavioral and physiological thermoregulation of crocodilians. Amer. Zool. 19: 239-247.

Soule, M. 1963. Aspects of thermoregulation in nine species of lizards from Baja California. Copeia 1963(1): 107-115.

Spellerberg, I. F. 1972a. Temperature tolerances of Southeast Australian reptiles examined in relation to reptile thermoregulatory behavior and distribution. Oecologia 9: 23-46.

_____. 1972b. Thermal ecology of allopatric lizards (*Sphenomorphus*) in Southeast Australia. I. The environment and lizard critical temperatures. Oecologia 9: 371-383.

_____. 1972c. Thermal ecology of allopatric lizards (*Sphenomorphus*) in Southeast Australia. II. Physiological aspects of thermoregulation. Oecologia 9: 385-398.

_____. 1972d. Thermal ecology of allopatric lizards (*Sphenomorphus*) in Southeast Australia. III. Behavioral aspects of thermoregulation. Oecologia 11: 1-16.

Spotila, J. R., O. H. Soule, and D. M. Gates. 1972. Biophysical ecology of the alligator-heat energy budgets and climate spaces. Ecology 53(6): 1094-1102.

Spray, D. C. 1974. Characteristics, specificity, and efferent control of frog cutaneous cold receptors. J. Physiol. 237(1): 15-38.

_____, and D. B. Belkin. 1972. Heart rate-cloacal temperature hysteresis in iguana is a result of thermal lag. Nature 239: 337-338.

_____, and D. B. Belkin. 1973. Thermal patterns in the heating and cooling of *Iguana iguana* and *Ctenosaura hemilopha*. Comp. Biochem. Physiol. 44A(3): 881-892.

Stainsby, W. N. and J. K. Barclay. 1970. Exercise metabolism: O_2 deficit, steady level O_2 uptake, and O_2 uptake for recovery. Med. Sci. Sports 2(4): 177-181.

Stebbins, R. C. 1943. Adaptations in the nasal passages for sand burrowing in the saurian genus *Uma*. Amer. Nat. 77: 38-52.

_____, and R. W. Barwick. 1968. Radiotelemetric study of thermoregulation in the lace monitor. Copeia 1968(3): 541-547.

Stewart, G. R. 1965. Thermal ecology of the garter snake *Thamnophis sirtalis concinnus* (Hallowell) and *Thamnophis ordinoides* (Baird and Girard). Herpetologica 21(2): 81-102.

Strunk, T. H. 1971. Heat loss from a newtonian animal. J. Theor. Biol. 33: 35-61.

Tanner, W. W. and J. E. Krogh. 1974. Variations in activity as seen in four sympatric lizard species of Southern Nevada. Herpetologica 30(3): 303-308.

Taylor, C. R., S. L. Caldwell, and J. J. Rowntree. 1972. Running up and down hills: Some consequences of size. Science 178: 1096-1097.

Templeton, J. R. 1970. Reptiles. Pp. 167-221. *In* G. C. Whittow, ed., Comparative physiology of thermoregulation, Vol. 1. Academic Press, New York. 333 p.

_____. 1971. Peripheral and central control of panting in the desert iguana, *Dipsosaurus dorsalis*. J. Physiol. Paris 63: 439-442.

Thauer, R. 1970. Thermosensitivity of the spinal cord. Chap. 33. *In* J. D. Hardy, A. P. Gagge, and J. A. J. Stolwijk, eds., Physiological and behavioral temperature regulation. Charles C. Thomas, Springfield, Illinois. 944 p.

Vance, V. J. 1973. Temperature preference and tolerance in the gecko, *Coleonyx variegatus*. Copeia 1973(3): 615-617.

Van Mierop, L. H. S. and S. M. Barnard. 1976. Observations on the reproduction of *Python molurus bivittatus* (Reptilia, Serpentes, Boidae). J. Herpetol. 10(4): 333-340.

Vaughn, L. K., H. A. Bernheim, and M. J. Kluger. 1974. Fever in the lizard *Dipsosaurus dorsalis*. Nature 252: 473-474.

Vernberg, F. J. and R. E. Tashian. 1959. Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca* I. Thermal death limits. Ecology 40(4): 589-593.

Vernon, J. and J. Heatwole. 1970. Temperature relations of the water skink, *Sphenomorphus quoyi*. J. Herpetol. 4(3-4): 141-153.

Weathers, W. W. 1970. Physiological thermoregulation in the lizard *Dipsosaurus dorsalis*. Copeia 1970(3): 549-557.

_____. 1971. Some cardiovascular aspects of temperature regulation in the lizard *Dipsosaurus dorsalis*. Comp. Biochem. Physiol. 40A(2): 503-515.

_____. 1972. Influence of water vapour on the apparent capacity for physiological thermoregulation in reptiles. J. Comp. Physiol. 81: 301-308.

_____, and K. R. Morgareidge. 1971. Cutaneous vascular responses to temperature change in the spiny-tailed iguana, *Ctenosaura hemilopha*. Copeia 1971(3): 548-551.

Webb, G. J. W., C. R. Johnson, and B. T. Firth. 1972. Head-body temperature differences in lizards. Physiol. Zool. 45(2): 130-142.

_____, and G. J. Witten. 1973. Critical thermal maxima in turtles. Comp. Biochem. Physiol. 45A(3): 829-832.

Werner, Y. L. 1969. Eye size in geckos of various ecological types (Reptilia: Gekkonidae and Sphaerodactylinidae). Israel J. Zool. 18: 291-316.

_____. 1972. Temperature effects on inner-ear sensitivity in six species of iguanid lizards. J. Herpetol. 6(3-4): 147-177.

White, F. N. 1973. Temperature and the Galapagos marine iguana-insights into reptilian thermoregulation. Comp. Biochem. Physiol. 45A(2): 503-514.

Wiewandt, T. A. 1977. Ecology, behavior, and management of the Mona Island ground iguana, *Cyclura stejnegeri*. Ph.D. Thesis. Cornell Univ. 338 p. Univ. Microfilms Int. Ann Arbor, Mich. (Diss. Abstr. 38(12): 5795B-5796B).

Wilhoft, D. C. 1958. Observations on preferred body temperature and feeding habits of some selected tropical iguanas. Herpetologica 14: 161-164.

_____. 1961. Temperature response in two tropical Australian skinks. Herpetologica 17(2): 109-113.

_____. 1966. The effect of thyroidectomy on the preferred body temperature of a lizard. Amer. Zool. 6(4): 601.

_____, and J. D. Anderson. 1960. Effect of acclimation on the preferred body temperature of the lizard, *Sceloporus occidentalis*. Science 131: 610-611.

Wilson, K. J. 1974. The relationship of oxygen supply for activity to body temperature in four species of lizards. Copeia 1974(4): 920-934.

_____, and A. K. Lee. 1974. Energy expenditure of a large herbivorous lizard. Copeia 1974(2): 338-348.

Windrow, S. L. 1977. Winter activity and behavior of the Exuman rock iguana, *Cyclura cychlura figginsi*. Unpub. M.S. Thesis, Rutgers Univ. 52 p.

Wit, A. and S. C. Wang. 1968. Temperature-sensitive neurons in preoptic/anterior hypothalamic region: Effects of increasing ambient temperature. Amer. J. Physiol. 215(5): 1151-1159.

Zotterman, Y. 1953. Special senses: Thermal receptors, Pp. 357-372. *In* V. E. Hall, J. M. Crismon, and A. C. Giese, eds., Annual review of physiology, Vol. 15. Annual Reviews, Inc., Stanford, California. 558 p.

BIOGRAPHICAL SKETCH

David Leslie Auth was born on July 7, 1945, in Plainfield, New Jersey. His family moved almost immediately to Wilmette, Illinois, where he spent practically all of the next 22 years. He graduated in 1963 from New Trier Township High School and from Northwestern University in 1967. He entered the University of Florida in the fall of 1967 and received the Master of Science degree in zoology in June of 1969. Drafted during the war in Vietnam, he spent the next four years in the United States Navy, first as a cryptologic technician with the Naval Security Group in Puerto Rico, then as a drug counselor at the Naval Drug Rehabilitation Center in Jacksonville, Florida. He returned to the University of Florida in January of 1974 and has continued work toward the Doctor of Philosophy to the present time.

He is a member of the American Association for the Advancement of Science, the American Institute of Biological Sciences, the American Society for Ichthyologists and Herpetologists, the Ecological Society of America, and Phi Kappa Phi.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Walter Auffenberg, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Archie Carr
Graduate Research Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John H. Kaufmann
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Brian K. McNab
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Hugh L. Popenoe
Professor of Soils Science

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

April, 1980

Dean, Graduate School

UNIVERSITY OF FLORIDA
3 1262 08667 042 8